

AN EVALUATION OF THE GENUS *TETHYA* (PORIFERA: DEMOSPONGIAE: HADROMERIDA) WITH DESCRIPTIONS OF NEW SPECIES FROM THE SOUTHWEST PACIFIC.

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ABSTRACT

A review and redefinition of descriptive terminology and specific diagnostic characters in the genus *Tethya* has allowed an evaluation of the status of *Tethya* and construction of a descriptive framework through which new species can be recognised. Descriptions of eleven new species of *Tethya* from New Zealand, Australia, Papua New Guinea and New Caledonia are given in conjunction with redescrptions of *Tethya aurantium*, *T. seychellensis* and *T. robusta*. Suggestions for a new approach to the systematics of *Tethya* are put forward.

KEYWORDS: Porifera, Demospongiae, Hadromerida, Tethyidae, *Tethya*, new species, taxonomy, phylogenetics.

INTRODUCTION

This communication reports 11 new species of the genus *Tethya* (Class Demospongiae, Subclass Tetractinomorpha, Order Hadromerida, Family Tethyidae) and provides redescrptions and re-evaluations of several species of this genus.

At present there are a number of large demosponge genera which obviously contain several generic entities or groups, eg. *Haliclona* (Bergquist and Warne 1980), *Halichondria*, *Hymeniacidon*, *Axinella* (Bergquist *et al.* 1980, 1985). The difficulty is not in recognizing such problem areas but in coming forward with new information and new approaches which can resolve the composition of such genera (Bergquist and Wells 1983). *Tethya* is potentially one such genus. The descriptions of the new species which follow provide a framework within which some suggestions for subdivision of the genus can be developed.

We must note that this work has been many years in preparation and, during the period that one of us has set this topic aside, Sarà (1987) has turned his attention to the genus and his studies have provided a useful framework. This contribution should assist in the general and joint aim of identifying characters which define groups of species presently clustered within the genus *Tethya*.

BACKGROUND

A major problem in comparing descriptions of sponges generated by different authors over nearly two centuries is terminology and the way it is applied. This is particularly so in the case of the microscleeres in *Tethya* and it also applies to regional differentiation in the soft tissues and to features of the sponge surface. Imprecision in terminology must be resolved before descriptive data can be used reliably in taxonomic analyses as raw material for cladistic and biogeographic studies. We have included diagrammatic and photographic material in support of the systematic descriptions sufficient to make our terminology clear.

Spicule terminology. The shape, localization and function of spicules in the genus *Tethya* are characters of diagnostic value. An attempt is made here to develop a consistent terminology for description of these spicules.

Megascleeres: The megascleeres that radiate from a basal centrum to produce the characteristic tethyid skeleton are termed stronglyloxeas. A stronglyloxea is a monactinal spicule which differs from a style only in the asymmetry and irregularity of both the proximal (stylo/strongylo) and distal (oxeote) extremities. Such irregularities are denoted here by the prefix aniso:

isostrongyloxeas preserve the classical shape at both extremities. Stepping rather than tapering at the distal extremity can also occur. The spicules can be straight, curved or flexuous. We find that these morphologies are frequently species specific and as such should be included in the description of megasclere complement.

The arrangement of megascleres in tracts and brushes, and the arrangement of these structures in the cortex and at the sponge surface, provide consistent diagnostic characters and thus valuable information when assessing the relationships between species (e.g. Fig. 16). Megasclere tracts in some species continue from choanosome to cortex remaining uniform in size over their length (*T. bullae*, Fig. 23; *T. murtoni*, Fig. 21). In contrast, there are species of *Tethya* in which tracts radiate within the cortex, with a range of branching patterns from non-branched and solid (*T. stolomifera*, Fig. 18; *T. aurantium*, Fig. 16), to secondary (*T. seychellensis*, Fig. 31) or elaborate tertiary branching (*T. popae*, Fig. 27; *T. communis*, Fig. 43). In addition to radiating non-branched megasclere tracts *T. aurantium* has an erect palisade of spicules that crown each tract and protrude through the sponge surface. Sponges with branching megasclere brushes usually also have radially disposed interstitial megascleres in the choanosome.

Microscleres: The microscleres of *Tethya* are of two major types - megasters, which include oxyspherasters and oxyasters, and micrasters. Oxyspherasters (Figs 1-4) occur predominantly in the cortex but can extend in attenuated numbers into the choanosome. These spicules have a large centrum with rays that are usually shorter than the centrum diameter. We recognize consistently three forms of oxyspheraster in *Tethya* based on the morphology of the ray and its tip in addition to the ratio of oxyspheraster ray length to centrum diameter. Oxyspherasters have oxete ray tips with a conical (Figs 1-2), or a concave (Fig. 3) ray profile. Mammillate oxyspherasters have a convex ray profile (Fig. 4).

Oxyasters are restricted to the choanosome. These spicules are distinctive in that they have little or no centrum development and frequently very few rays. These rays are either unbranched (Fig. 5), bifurcate with smooth or spined ray tips (Figs 6a-b), or terminally branched (Fig. 6c). Rays can be curved or angulate.

Micrasters (Figs 7-12) are smaller than oxyspherasters and oxyasters. This term embraces a variety of small spicules that pack the surface epithelium of the sponge and line canals in the

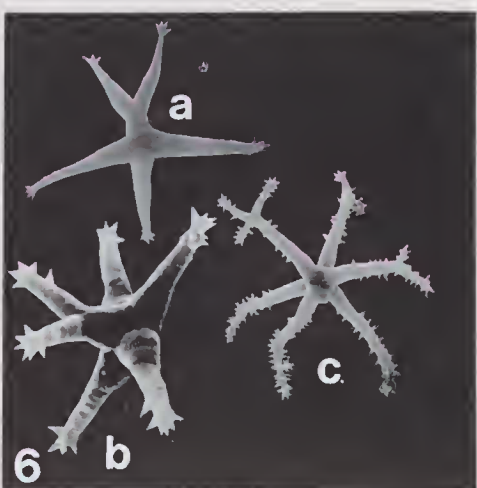
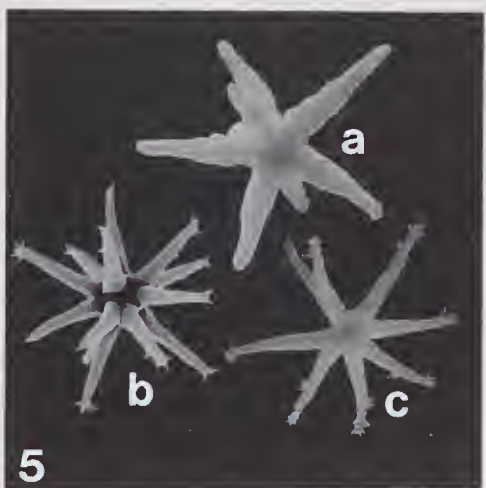
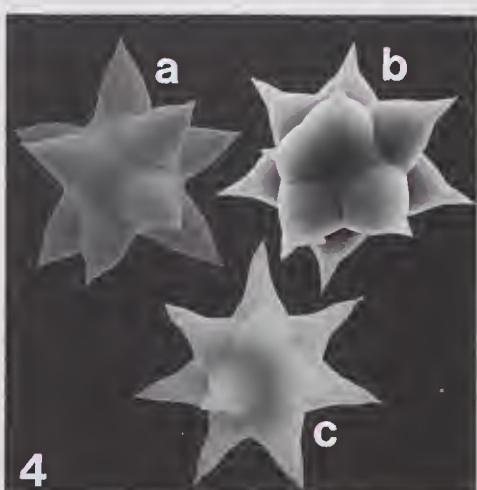
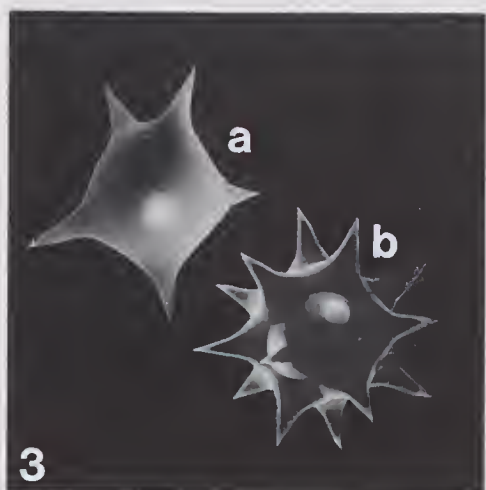
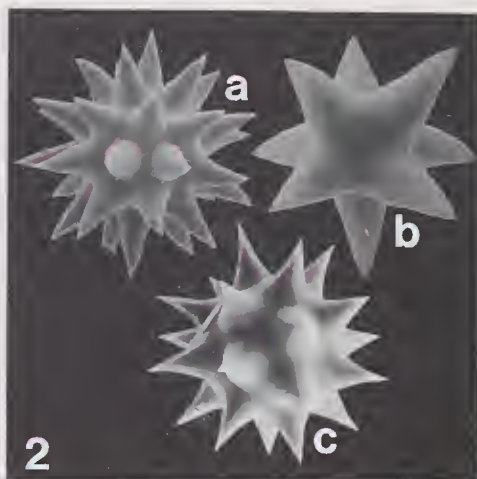
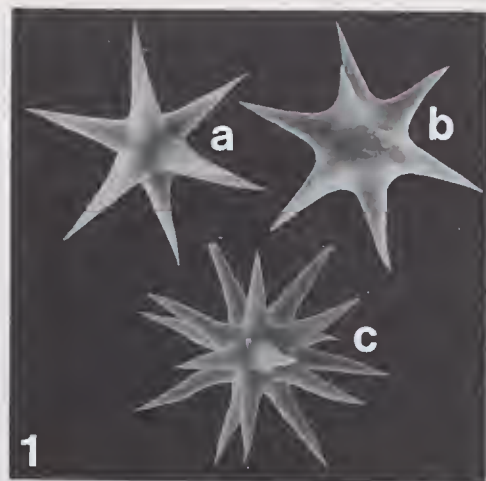
cortex and choanosome. Intraspecific variation in the shape of these spicules is low. This justifies redefinition of the micraster categories that have been used hitherto (Burton 1924; Topsent 1918; de Laubenfels 1950; Sarà and Gaino 1987; Sarà 1987). Our redefinition of micraster morphology is based on the shape of the ray tip independent of any ornamentation such as spining that may also be present. The ray tip profile thus becomes an important diagnostic character for the differentiation of species in *Tethya*.

Tylasters have a tylote ray tip which is often heavily spined (acanthotylasters) (Fig. 7). Strongylasters have a strongylote ray tip and these are often only lightly spined (acanthostrongylasters) (Fig. 8). The ray tips of chiasters are truncate and short, also often heavily spined (acanthochiasters) (Fig. 9). Oxyspherasters have a centrum and oxete ray tips, rays are usually smooth or lightly spined and comparatively long (acanthooxyspherasters) (Fig. 10). By referring to this latter form of micraster as an *oxyspheraster*, rather than an *oxyaster*, we wish to make the distinction between oxete micrasters and the megaster-type oxyaster which is confined to the choanosome of only a few species of *Tethya*, and which is later shown to be an important character in distinguishing groups of species within *Tethya*.

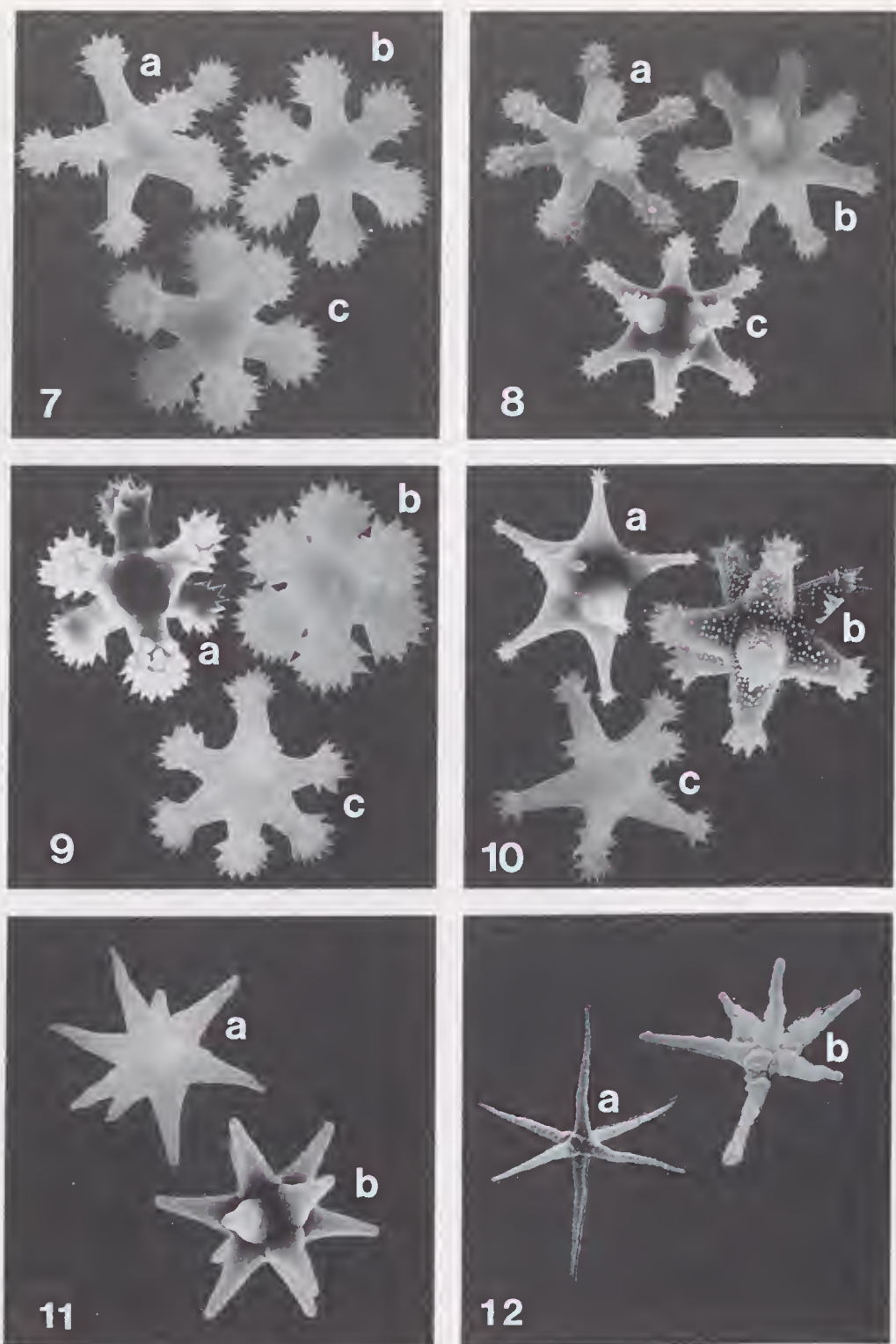
Microoxyspherasters are extremely small oxyspherasters with conical rays (Fig. 11). Microoxyasters are extremely small oxyasters usually with unspined rays (Fig. 12).

All micrasters can vary in the degree of spination along the ray and at the ray tip, the length of rays and spines, and in the relative degree of centrum development. These appear to be constant features within species but are difficult to describe in an objective way. The average dimensions of micrasters and the number of rays on asterose microscleres has generally been acknowledged to be variable.

Using the above definitions closely related species such as *Tethya aurantium* and *T. citrina* (Sarà and Gaino 1987) become easier to differentiate on the basis of their micraster content. For example, the "cortical tylasters and chiasters" of *T. aurantium* (Sarà and Gaino 1987: Fig. 2a-e) and *T. citrina* (Sarà and Gaino 1987: Fig. 3a-e) become acanthotylasters (Sarà and Gaino 1987: Fig. 2a) and acanthostrongylasters (Sarà and Gaino 1987: Fig. 2b-c) in *T. aurantium* and only acanthostrongylasters in *T. citrina*. In a case such as this where there is little recorded difference in spicule size between the two species, a strict



Figs 1-6. Microscleres of *Tethya*. Refer to text for relative sizes: **1**, long-rayed conical oxyasterasters in *Tethya mortoni* (a), *Tethya aurantium* (b) and *Tethya bullae* (c); **2**, short-rayed conical oxyasterasters in *Tethya coccinea* (a), *Tethya communis* (b) and *Tethya sollasi* (c); **3**, concave oxyasterasters in *Tethya stolonifera* (a,b); **4**, mammillate (convex) oxyasterasters in *Tethya stolonifera* (a,b) and *Tethya aurantium* (c); **5**, unbranched oxyasterasters in *Tethya communis* (a), *Tethya pellis* (b) and *Tethya australis* (c); **6**, branched oxyasterasters in *Tethya fastigata* (a), *Tethya amplexa* (b) and *Tethya seychellensis* (c).



Figs 7-12. Microscleers of *Tethya*. Refer to text for relative sizes; 7, acanthotylasters in *Tethya pellis* (a), *Tethya seychellensis* (b) and *Tethya fastigata* (c); 8, acanthostrongylasters in *Tethya popae* (a), *Tethya coccinea* (b) and *Tethya stolonifera* (c); 9, acanthochiasters in *Tethya seychellensis* (a), *Tethya fastigata* (b) and *Tethya pellis* (c); 10, acanthooxyspherasters in *Tethya stolonifera* (a,c) and *Tethya bullae* (b); 11, microoxyspherasters in *Tethya stolonifera* (a,b); 12, microoxyasters in *Tethya seychellensis* (a) and *Tethya popae* (b).



Figs 13-14. Polyrhabs of *Tethya communis*. Refer to text for relative sizes: 13, regular rods; 14, angulate rods.

definition of spicule shape permits differentiation.

In *Tethya communis* there is an additional micraster type which we have termed the polyrhabd. These spicules are usually microspined rods with strongylote or tylote ends, they can be multirayed with rays of different lengths (Fig. 13), and can be angulate along the main axis (Fig. 14).

The colour notation for living and preserved specimens follow Munsell (1942). Collection localities are given in Figure 15. Spicule dimensions are given as mean length (range of length measurements) x mean width (range of width measurements) followed by the number of spicule measurements taken. All type material has been deposited in the Australian Museum (AM), Sydney, Australia and register numbers are cited in the text. Other abbreviations: BMNH, The Natural History Museum, London; UAZA, Zoology Department, University of Auckland, Auckland; USNM, United States National Museum, Washington; YPM, Peabody Museum of Natural History, Yale University; SUZS, Zoology Department, Sydney University, Sydney.

SYSTEMATICS

Order Hadromerida Topsent Family Tethyidae Gray

Tethyidae Gray, 1867:492

Diagnosis. Massive spherical to thickly encrusting or mounded Hadromerida with strict

radial megasclere skeleton composed of monaxon megascleres in tracts and brushes. A distinct cortical region marked by strong collagen deposition is always present but developed to a greater or lesser degree. Megascleres are strongyloxeas that can have markedly asymmetrical ends. Microscleres are oxyspherasters, oxyasters and micrasters in varying combinations.

Genus *Tethya* Lamarck

Tethya Lamarck, 1814:69

Alema Wright, 1881:15

Donatia Nardo, 1833:522

Tethyorrhaphis Lendenfeld, 1888:52 (*comb. nov.*)

Diagnosis. Spherical to semispherical Tethyidae with perfectly radial skeleton dominated by tracts of megascleres that emanate from a solid spicule centrum. Tracts remain uniform in diameter or diverge into brushes which can branch in the collagenous solid or lacunar cortical region. Tracts can be supplemented with interstitial choanosomal megasclere brushes that are basally situated, peripheral in the choanosome, or dispersed throughout the choanosome. The sponge surface is patterned by blunt conules or by polygonal tubercles of variable size separated by pore areas. Megascleres are strongyloxeas. Microscleres include oxyspherasters, branched or unbranched oxyasters, micrasters which include acanthose tylasters, chiasters, strongylasters, oxyspherasters, microoxyspherasters, microoxyasters and polyrhabs. *Tethya* species reproduce asexually

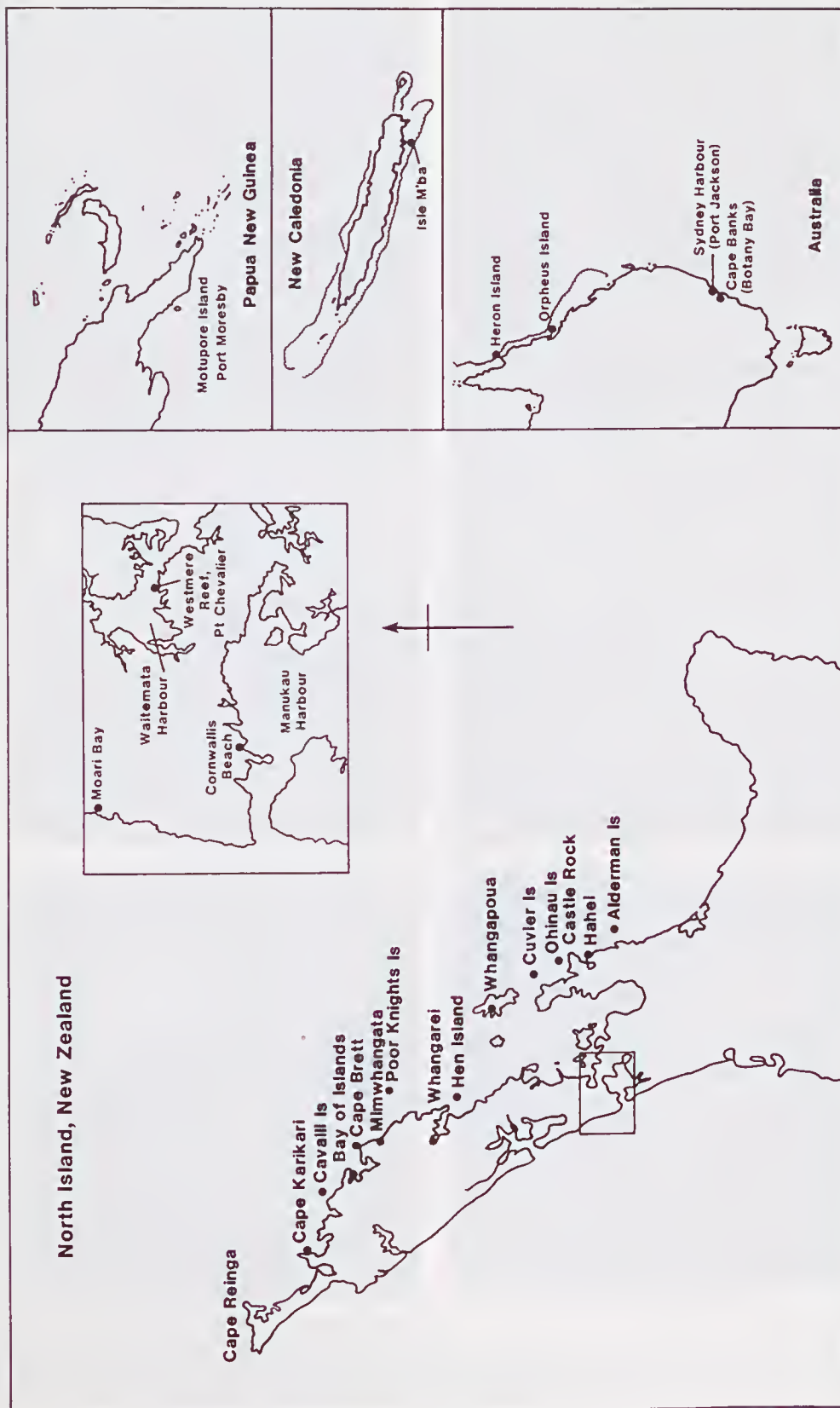


Fig. 15. Collection localities.

by production of both internal and external buds and sexually by production of parenchymella larvae following extrusion of eggs and sperm.

Tethya anrantium (Pallas)

(Figs 1b, 4c, 16)

Alcyonium aurantium Pallas, 1776:357.

Tethya aurantium - Topsent 1900:294.

Donatia lyncurium - Burton 1924:1036.

Tethya deformis - (pars) Burton 1924:1036.

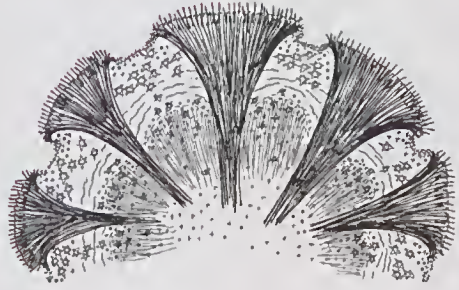
Tethya aurantium- Bergquist 1968:35.

Material examined. UAZA 1.2, 1.3: Cornwallis Beach, Manukau Harbour, Auckland, 174°36'E, 37°01'S, 0-2m, 2 specimens, 14 October 1990; UAZA 4.1, 4.6: Maori Bay, West Auckland, 174°27'E, 36°51'S, 0-1m, 1 specimen, 25 October 1988; UAZA 6.9: Ohinau Island, northern New Zealand, 175°52'E, 36°44'S, 10m, 2 specimens, 6 December 1988; UAZA 9.13: Monterey Bay, California, 121°55'W, 36°37'N, intertidal, 1 specimen, 5 March 1990.

Comparative material. *Tethya deformis* Burton, 1924 (BMNH 57.1.17.5).

Description. Sponge is spherical, 5mm to 59mm in diameter with a basal attachment disc or small solid roots. The surface is mammillate to tuberculate with elevations separated by pore grooves. The texture is firm, just compressible and microhispid to the touch. The exterior colour in life is cadmium orange (5.0YR7/10 to 7/12) or golden yellow (2.5Y8/10 to 8/12) and internal colour oxide yellow (10.0YR7/8 to 6/8). In ethanol the colour is yellow white (5.0Y9/4) to apricot (7.5YR7/6).

Skeleton. Widely spaced megasclere tracts 440 to 680µm in maximum diameter radiate sharply in the outer half of the one to three mm deep cortex to form inverted cone shaped brushes (780 to 1660µm diameter) (Fig. 16). In larger specimens megasclere tracts are widely spaced and cortical brushes are up to 3000µm wide. Cortical brushes terminate below the surface and radially dispersed megascleres emanate from these brushes to form a thin palisade of projecting spicules. Interstitial megascleres are abundant in the upper choanosome and are radial in orientation. Micrasters form a dermal crust and are abundant below this in the upper half of the cortex. Micrasters are abundant at and below the cortex-choanosomal boundary. The deeper region of the cortex is extremely collagenous and extends around the megasclere tracts into the choanosome to form a scalloped boundary.



16

Fig. 16. *Tethya aurantium*: general skeletal arrangement.

Micrasters are rare in the lower cortex. Oxyspherasters occur in the upper cortex, forming occasional perpendicular tracts of single spicules through the lower cortex to the upper choanosome where they are frequently more abundant. Oxyspherasters are common in the inner choanosome. In deep water specimens microscleres are less abundant than in intertidal specimens.

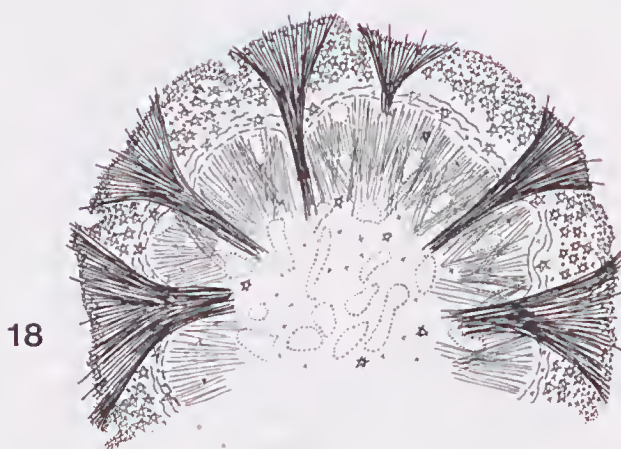
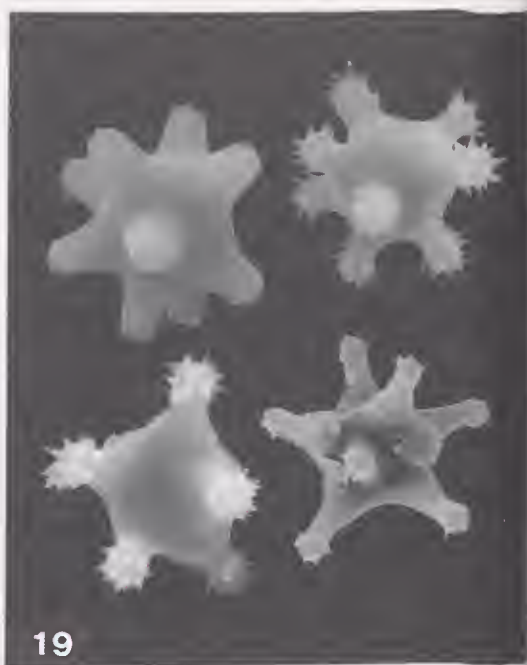
Spicules. Megascleres: Anisostrongyloxeas, proximal ends strongylote, distal ends hastate oxeote. Spicules are centrally thickened; 1189(478-1739) × 17(9-26)µm, n=20.

Microscleres: Megasters: oxyspherasters, occasionally mammillate (Fig. 4c), rarely concave with long fine rays (Fig. 1b); 49(31-67)µm, n=20. **Micrasters:** acanthooxyspherasters, acanthostrongylasters, occasionally acanthotyasters; 11(7-14)µm, n=20, microoxyasters; 4(3-5)µm, n=5, microoxyspherasters with double pointed ray tips; 4(3-5)µm, n=5.

Ecology. *Tethya anrantium* can be solitary or is clustered in groups of 2 to 20 individuals that are discrete but attached by broad short basal stolons. The sponge is found in crevices and under overhangs on rocky reef platforms, or on the tops of boulders covered by algae. In the subtidal individuals are common on most rocky reef faces, in light or in semi-shade.

Remarks. No substantial differences can be found between material from Monterey Bay, California, Torbay on the British coast, New Zealand specimens examined here, and descriptions of *Tethya aurantium* in the literature.

The micraster categories of *Tethya aurantium* have received attention recently with the observation by Sarà and Gaino (1987) that *T. aurantium* has two distinct sets of micrasters, one that con-



Figs 17-19. *Tethya stolonifera*: 17, preserved specimen, scale = 1 cm; 18, general skeletal arrangement; 19, centrum development in microasters.

sists of 'ehiasters' (acanthostrongylasters, see Sarà and Gaino 1987: 315, Fig. 2b-c) and tylasters in a dermal layer, and another, a set of 'uniform oxyasters' occurring in the middle to lower cortex and extending into the choanosome. Sarà and Gaino differentiate these spicules by size as well as morphology. This pattern was observed in

several New Zealand specimens of *Tethya aurantium* but it was not as precise as Sarà and Gaino's work indicated.

We have not emphasised dispositional and dimensional differences between micraster categories in this work. Such differentiation is not evident in most of the material examined here.

with the exception of *Tethya fastigata* and *T. amplexa* where deformed acanthochiasters are found more frequently in a cortical dermal layer than in the lower cortex or choanosome. For closely related species, however, differences in disposition of micraster types could provide additional useful characters for species separation as Sarà and Gaino indicate.

It is also our experience that micraster categories in all species examined have characteristic dimensions - acanthoospherasters are consistently longer rayed, hence larger, than acanthostrongylasters, acanthotylasters and acanthochiasters. We suggest therefore that Sarà and Gaino's oxyasters are actually acanthoospherasters as *Tethya aurantium* does not contain true oxyasters in the sense of Dendy (1921), where oxyasters are defined as lacking a centrum and having frequently curved or branched oxeote rays. Oxyasters are significantly larger than micrasters and are confined to the choanosome. Attention to these distinctions will avoid confusion in any future analysis of the microsclere complement of *Tethya aurantium*.

Distribution. Atlantic coast of Europe, Africa, South America, New Zealand, Mediterranean.

Tethya stolonifera sp. nov.

(Figs 3a-b, 4a-b, 8c, 10a,c, 11a-b, 17, 18, 19, Pl 1a-e).

Type Material. HOLOTYPE - AM Z5000: Westmere Reef, Waitemata Harbour, Auckland, New Zealand, 174°42'E, 36°51'S, 0-0.5m, 2 February 1988.

Additional material. UAZA 7.1, 26 August 1989, UAZA 9.5, 1 February 1972, UAZA 9.15, 16 October 1974, UAZA 9.4, 30 December 1990: Westmere Reef, Waitemata Harbour, Auckland, 174°42'E, 36°51'S, 0-0.5m, 5 specimens; UAZA 9.16, 4 June 1974, UAZA 8.9, 4 June 1974: Mill Bay, 174°37'E, 37°00'S, and Cornwallis Beach, Manukau Harbour, Auckland, 174°36'E, 37°01'S, 0-1.5m, 5 specimens.

Description. A perfectly spherical to sub-spherical sponge 3 to 11mm in diameter with extensive basal stolons from which numerous buds arise (Fig. 17, Pl. 1a). The surface is dissected into circular or polygonal areas by a system of pore grooves. Oscules are dispersed on tubercles flush with the sponge surface elevated above pore grooves. Texture soft, compressible in life. Colour of the cortex in life is reddish yellow (2.5Y8/10 to 2.5Y8/12) and the choanosome is yellow

brown (10.0YR7/10 to 10.0YR6/8). In ethanol the sponge is orange brown (10.0YR7/4) throughout. *Tethya stolonifera* reproduces asexually by stolon budding, but internalized buds have also been found occasionally in this species.

Skeleton. Well separated narrow megasclere tracts 200 to 425µm wide radiate through a cavernous endosome (Fig. 18). Tracts radiate in the cortex to form inverted cone-shaped brushes 1000 to 1500µm wide. Megasclere tracts are frequently strongly spiralled about the solid spicule core. Spicules can protrude through the surface. Interstitial spicule brushes form a dense radiating sub-cortical band. The cortex is 200 to 1300µm deep and extends into the choanosome around megasclere tracts to produce a scalloped boundary. The deeper region of the cortex is strongly collagenous. Micrasters are packed in a surface layer 25 to 50µm deep and are abundant subdermally in the cortex. Oxspherasters are present in moderate abundance throughout the cortex. Micrasters and oxyspherasters decrease in density in the lower 100 to 200µm of the cortex and are occasional in the choanosome.

Spicules. Megascleres: Anisostrongyloxeas, proximal ends strongylote, distal ends fusiform or hastate oxeote; 741(218-1225)×16(8-26)µm, n=20.

Microscleres. Megasters: Oxyspherasters, mammillate (Fig. 4a,b), conical and concave (Fig. 3a,b) in equal numbers; 39(13-76)µm, n=20.

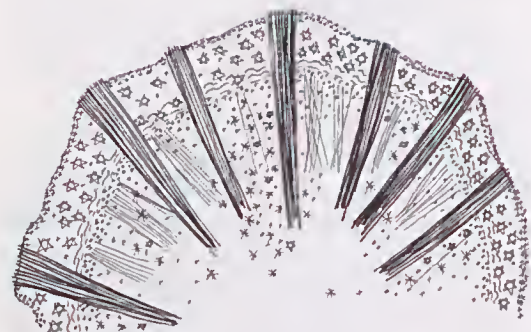
Micrasters: acanthostrongylasters with reduced spining and large centurms (Fig. 8c), acanthoospherasters with small centurms (Fig. 10a,c), acanthotylasters and with long spines and large centurms (Fig. 19); 12(8-14)µm, n=10, rare microoxyspherasters (Fig. 11a,b); 6(3-10)µm, n=10.

Ecology. Sponges are discrete but are attached by long basal stolons in turfing coralline algae on intertidal basalt boulders, or in crevices in shallow subtidal to intertidal rocky reef platforms in sheltered bays.

Remarks. Other species of *Tethya* that resemble *T. stolonifera* in some features are *T. norvegica* Bowerbank and *T. deformis* Thiele. *Tethya norvegica* is a small sponge with a thin cortex containing large cavities and megasclere tracts that radiate in the cortex (Bowerbank 1872). A specimen identified as *T. norvegica* (BMNH 77-5-21-152) from Norway is comparable to *T. stolonifera* in the arrangement of megasclere tracts which form inverted cone shaped, unbranched brushes in the cortex, but interstitial

megaseleres in this specimen are present throughout the choanosome. The specimen of *T. norvegica* differs dramatically from *T. stolonifera* in spiculation: oxyspherasters in *T. norvegica* are rare, 21 to 38 μm in diameter, with long conical rays that are often severely truncated, and megaseleres are 784 to 1379 μm in length. In *T. norvegica* micrasters have very fine long rays and are completely lightly microspined acanthooxyspherasters and acanthostrongylasters.

Tethya deformis Thiele resembles *T. stolonifera* in having lightly spined acanthostrongylasters that show some centrum development and a strong spiraling of megasclere tracts around a solid spicule core (Thiele 1898). The two species differ in megasclere size (*T. deformis*: 1300–1850 μm ; Thiele 1898) and body form, *T. deformis* being irregularly lumpy, flattened and elongate rather than spherical. Micraster centrum development is not as marked in *T. deformis* as it is in *T. stolonifera*.



Figs 20–21. *Tethya mortoni*: 20, preserved specimen, scale = 1 cm; 21, general skeletal arrangement.

Tethya monstrosa (Burton, 1924) from Tasmania has oxyspherasters of three morphologies and micrasters that have large centruns, frequently reduced ray numbers and ray spination, as do the comparable spicules of *T. stolonifera*. However, *T. monstrosa* also contains oxyasters and has microseleres that pack both the cortex and the choanosome (Burton 1924).

Tethya stolonifera is similar to *T. aurantium* in general skeletal arrangement with both species having sharply radiating unbranched megasclere tracts and interstitial megaseleres in the outer choanosome. The two species differ considerably in details of spicule morphology, dimensions and disposition, in body size, surface structure, colouration, and in mode of asexual reproduction.

Etymology. The species name emphasises the capability for development of an extensive basal stolon system.

Tethya mortoni sp. nov.
(Figs 1a, 20, 21)

Type Material. HOLOTYPE - AM Z5073: Cornwallis Beach, Manukau Harbour, Auckland, New Zealand, 174°36'E, 37°01'S, 0–0.5m.

Additional material. UAZA 8.4c: Cornwallis Beach, Manukau Harbour, Auckland, New Zealand, 174°36'E, 37°01'S, 0–0.5m, 5 specimens, 22 July 1988.

Description. An ovoid sponge six to eight mm in diameter and 8 to 12mm rising from a basal attachment disc (Fig. 20). The surface is divided into low tubercules. There is a single or double apical oscule. The texture is firm, just compressible in life. Exterior colour in life is maize yellow (2.5Y8/10), interior is brown yellow (7.5YR7/10). In ethanol the sponge is yellow white (2.5Y8/12) throughout. This species reproduces by the asexual production of buds on erect tissue filaments 0.5 to 1.0mm thick and one to two mm long.

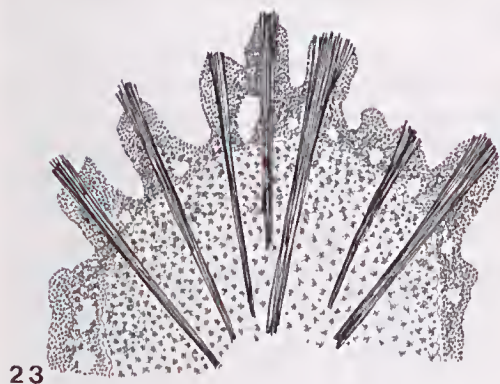
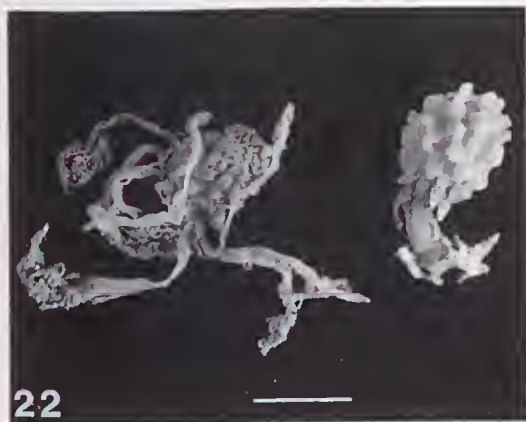
Skeleton. Fine megasclere tracts 122 to 490 μm wide radiate from the centre of the sponge, expanding slightly within the cortex, spicules only just protrude beyond the sponge surface (Fig. 21). Sparse interstitial megaseleres are disposed radially at irregular intervals in the upper choanosome. The cortex is 245 to 490 μm deep and the lower quarter is strongly collagenous but shows no lessening of spicule density. Micrasters form a dermal layer and are abundant below the cortex-choanosomal boundary, attenuating in number into the choanosome. Micrasters and short-rayed oxyspherasters are moderately dense

below the dermal layer and throughout the cortex. Micrasters and larger, long-rayed oxyspherasters are abundant but irregularly distributed in the deeper choanosome. Short-rayed oxyspherasters occur in the cortex and choanosome but decrease in number in the upper third of the choanosome.

Spicules. Megascleres: Anisostrongyloxeas, proximal ends strongly notched, distal ends fusiform oxeate; $735(384-1092) \times 17(10-21) \mu\text{m}$, $n=20$.

Microscleres: Megasters: Choanosomal conical long-rayed oxyspherasters with small centurms (Fig. 1a); $48(26-62) \mu\text{m}$, $n=20$, cortical short-rayed oxyspherasters with large centurms $38(28-52) \mu\text{m}$, $n=20$. **Micrasters:** short spined acanthostrongylasters, acanthotylasters with centrum development in 50% of spicules, occasional acanthooxyspherasters; $11(8-13) \text{mm}$, $n=10$, microoxyspherasters; $7(5-8) \mu\text{m}$, $n=50$, microoxyasters; $7(5-8) \mu\text{m}$, $n=5$.

Ecology. The sponge is solitary and grows deep in crevices on the sides of shallow subtidal rock platforms adjacent to deep water channels.



Figs 22-23. *Tethya bullae*: 22, preserved specimens, scale = 1 cm; 23, general skeletal arrangement.

Remarks. Although *Tethya mortoni* and *T. stolonifera* are similar in body size and occupy a comparable habitat, they differ markedly in skeletal architecture and spicule morphology. *Tethya mortoni* has megasclere tracts of uniform width, a thin cortex with moderately dense oxyspherasters, and long-rayed oxyspherasters in the choanosome. In these features *T. mortoni* is similar to the later described species *T. bullae*. *Tethya mortoni* has been recorded only from Cornwallis Beach, Manukau Harbour.

Etymology. This species is named after Professor J. E. Morton, Emeritus Professor of Zoology, University of Auckland.

Tethya bullae sp. nov.

(Figs 1c, 10b, 22, 23)

Type material. HOLOTYPE-AM Z5074: Alderman Islands, northern New Zealand, $176^{\circ}05'E$, $36^{\circ}58'S$, 100m, 2 February 1966.

Additional material. UAZA 9.8: West of Cape Reinga, New Zealand, $172^{\circ}40'E$, $34^{\circ}24'S$, 134m, 2 specimens, 15 October 1971; UAZA 9.7: Cuvier Island, New Zealand, $175^{\circ}45'E$, $36^{\circ}23'S$, 81m, 1 specimen, 8 July 1966.

Description. A spherical to ovoid sponge, 10 to 14mm in diameter, 11 to 20mm high, with basal flattened branched rooting processes (Fig. 22). The surface is raised into large blunt tubercles 1 to 2 mm high and wide supported by the extension of thick megasclere tracts which traverse the cortex. The surface is often partially covered with adherent pebbles and shell fragments. In life the sponge is barely compressible and is yellow gray (5.0Y7/2) in colour with a slightly paler cortex and tubercles. In ethanol, interior and cortical tissue between tubercles is reddish yellow (10.0YR7/6). *Tethya bullae* reproduces by the production of internal buds.

Skeleton. Isolated tracts of megascleres $500 \mu\text{m}$ wide traverse the choanosome and radiate slightly in the cortex where they support the marked surface tubercles (Fig. 23). Spicules can protrude well beyond the surface. Choanosome and cortex are packed with microscleres. The cortex is cavernous, 250 to $2500 \mu\text{m}$ deep, and densely packed with short-rayed oxyspherasters and micrasters, with the latter particularly dense in the peripheral $100 \mu\text{m}$. The choanosome is packed with large long-rayed oxyspherasters and micrasters, and the cortex-choanosomal boundary is extremely narrow, collagenous and aspiculous. Short-rayed oxyspherasters are particularly abundant in the outer choanosome.

Spicules. Megasccleres: Anisostrongyloxeas, slim strongylote proximal ends, hastate oxeote distal ends; $1361(350-2225) \times 20(8-30) \mu\text{m}$, $n=20$.

Microsccleres: Megasters: Choanosomal long-rayed oxyspherasters with slightly curved long fine rays, ray tips occasionally bifurcate (Fig. 1c); $110(83-166) \mu\text{m}$, $n=30$; cortical short-rayed oxyspherasters often with forked or truncated rays; $88(62-114) \mu\text{m}$, $n=20$. **Micrasters:** completely and finely microspined acantho-oxyspherasters (Fig. 10b), acanthostrongylasters; $14(11-15) \mu\text{m}$, $n=20$, microoxyspherasters; $9(9-10) \mu\text{m}$, $n=5$.

Ecology. The sponge is a solitary deep water species which occurs rooted in shell, mud and gravel substrate.

Remarks. *Tethya bullae* resembles *T. fissurata* Lendenfeld from Port Jackson, Australia, in that both species grow rooted in soft substrate and have a very pronounced tuberculate surface. The tubercles of *T. fissurata* are, however, large expanded inverted cones with terminal depressions (Hallmann 1914: Pl. XV, Fig. 3) while the tubercles of *T. bullae* are narrow, blunt and of uniform thickness.

Examination of slide material of *Tethya fissurata* (Dendy Collection: 25.11.1.1092) reveals that both *Tethya bullae* and *T. fissurata* have robust unbranched megasclere tracts, lack interstitial megasccleres and have long-rayed oxyspherasters which pack the choanosome. The two species differ in details of spiculation: the choanosomal oxyspherasters of *T. fissurata* are considerably larger than those of *T. bullae* (*T. fissurata*-mean diameter $176 \mu\text{m}$, range $94-285 \mu\text{m}$, $n=20$), and *T. fissurata* contains oxyasters. The micrasters of *T. fissurata* are of different morphology to those of *T. bullae*; micrasters in *T. fissurata* are acanthooxyspherasters and acanthochiasters with enlarged centurms, those of *T. bullae* are acantho-oxyspherasters and acanthostrongylasters. *Tethya bullae* reproduces by the production of internal buds. The reproductive mode for *T. fissurata* is unknown.

Tethya mortoni and *T. bullae* have a similar skeletal arrangement with unbranched, minimally radiating megasclere tracts, a multilayered cortex with microsccleres evenly distributed throughout, and large long-rayed oxyspherasters in the choanosome. This is an unusual and additional feature present in both *T. mortoni*, *T. bullae* and *T. fissurata*. The two species differ in general spicule density, with *T. bullae* having much greater spicule density, as well as in overall body morphology, surface structure, and in habitat.

Etymology. The species name refers to the distinctive surface tubercles.

Tethya australis sp. nov.
(Figs 5c, 24, 25, Plate 1b).

Tethya ingalli - Sollas 1888:431.

Donatia ingalli - Hentschel 1909:371.

Donatia diploderma - (pars) Burton 1924:1039.

Tethya ingalli - (pars) Burton 1956:120.

Tethya ingalli - Bergquist 1968:36.

Tethya ingalli - Wiedenmayer 1989:29.

Type material. HOLOTYPE - AM Z5086: Castle Rock, Whitianga, New Zealand, $174^{\circ}50'E$, $36^{\circ}50'S$, 26m, 8 December 1988.

Additional material. UAZA 1.1: Cornwallis Beach, Manukau Harbour, Auckland, $174^{\circ}36'E$, $37^{\circ}01'S$, 0-2m, 2 specimens, 17 March 1988; UAZA 6.6: Castle Rock, Whitianga, $174^{\circ}50'E$, $36^{\circ}50'S$, 20m, 2 specimens, 8 December 1988; UAZA 6.7: Ohinau Island, New Zealand, $175^{\circ}52'E$, $36^{\circ}44'S$, 10m, 3 specimens, 6 December 1988; UAZA 10: Whangaparapara, Great Barrier Island, New Zealand, $175^{\circ}20'E$, $36^{\circ}15'S$, 5m, 1 specimen, 3 December 1964.

Description. A spherical to ovate sponge, 20 to 25mm in diameter, with small attachment discs and thick basal roots (Fig. 24, Pl. 1b). The surface is irregularly mammillate to tessellated with buds arising on tissue filaments 2 to 10mm long. The texture is firm, just compressible, and the sponge is waxy to the touch. Oscules, in a group of three to four are situated apically and occasionally laterally. The external colour is deep rose pink (5.0R6/6), internally dull yellow (2.5Y7/4). In ethanol, pale pink (2.5YR7/4 to 7.5YR8/4) externally and dull yellow (7.5YR7/4) internally. This species reproduces asexually by the production of buds on tissue filaments in the period July to January.

Skeleton. This is made up of widely separated slim flexuous megasclere tracts, 171 to $612 \mu\text{m}$ in diameter, radiating into tertiary branches that terminate at the surface (Fig. 25). The cortex, 1340 to $2500 \mu\text{m}$ deep is traversed by radially disposed tracts of oxyspherasters and the cortex to choanosomal boundary is scalloped. Interstitial megasccleres form subradial to radial plumose brushes throughout the choanosome. Micrasters form a distinct dermal layer, 70 to $100 \mu\text{m}$ deep and this grades in lower density into the cortex. Oxyspherasters are abundant below the micraster layer. Internal to the oxyspheraster layer the deeper half to three-quarters of the cortex is relatively spicule free and strongly collagenous.

The choanosome contains abundant oxyasters and micrasters uniformly distributed throughout. Oxyspherasters form a conspicuous band just below the cortex-choanosomal boundary but attenuate in number towards the centre of the sponge. The density of oxyspherasters in the cortex and choanosome varies from moderately common in all shallow water specimens examined, to abundant in specimens from deeper water.

Spicules. Megasccleres: Anisostrongyloxeas, proximal ends strongylote, distal fusiform oxeote, frequently stepped; $960(291-1617) \times 11(5-18) \mu\text{m}$, $n=20$.

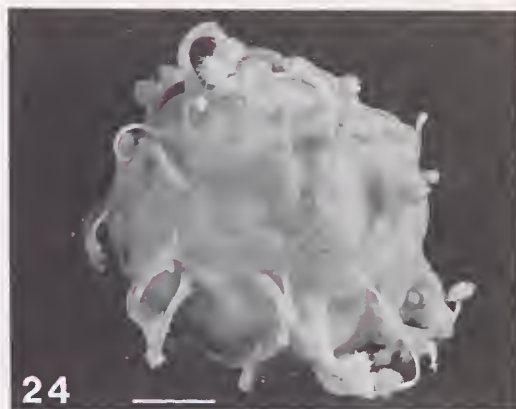
Microsccleres: Megasters: Oxyspherasters with a low number, as few as two to three, long conical slightly curved rays that are often reduced to rounded stumps, or rays can be completely absent leaving only a sphere. These spheres are commonly found in the deep choanosome: $36(18-52) \mu\text{m}$, $n=20$. Oxyasters, straight or curved with half the ray or only the ray tip spined, or smooth (Fig. 5c); $29(22-31) \mu\text{m}$, $n=20$. **Micrasters:** acanthotylasters, acantho-strongylasters; $15(10-17) \mu\text{m}$, $n=20$, micro-oxyasters $9(7-10) \mu\text{m}$, $n=10$.

Ecology. The sponge is solitary and found most commonly in the upper subtidal fringe amongst algae, but the species has been recorded to 26m depth. In deep water sponges are found on open rock faces.

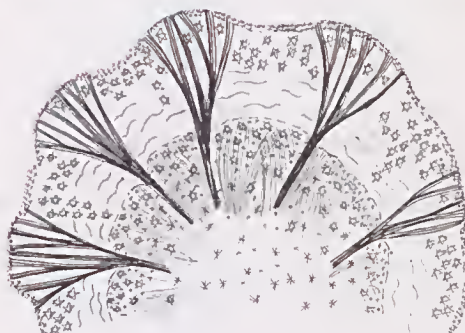
Remarks. *Tethya australis* is very similar to *T. ingalli* Bowerbank (1872) from Western Australia. Comparison of *T. australis* with the holotype of *T. ingalli* (BMNH 77-5-21-140) reveals a similar spicule morphology and skeletal arrangement. *Tethya ingalli* has megascclere tracts that branch in the cortex to form tertiary fans, has interstitial megasccleres throughout the choanosome and a scalloped cortex-choanosomal boundary, all as in *T. australis*.

The main differences between the two species are that *T. ingalli* has a cortex packed with oxyspherasters and lacks a surface micraster crust. In *T. australis* oxyspherasters are only moderately common and are concentrated in the outer and inner boundaries of the cortex and just below the cortex-choanosomal boundary. There is a slight reduction in oxyspheraster density in the lower third of the cortex in the holotype of *T. ingalli* but only in isolated patches. This feature is marked in *T. australis*. The choanosomal microsccleres of *T. ingalli* are evenly distributed and much less dense than in *T. australis*.

Whilst details of spicule morphology are extremely similar in the two species there are size



24



25

Figs 24-25. *Tethya australis*; 24, preserved specimen, scale = 0.5 cm; 25, general skeletal arrangement.

differences, oxyspherasters and oxyasters in *T. australis* are smaller than those in *T. ingalli* (oxyspherasters: $73(42-105) \mu\text{m}$; oxyasters: $33(26-39) \mu\text{m}$).

The general skeletal structure, spiculation, colouration and body morphology of specimens described as *Tethya ingalli* by Wiedenmayer (1989) from Bass Strait, South Australia, by Bergquist (1968) from New Zealand, and by Sollas (1888), Hentschel (1909) and Hallmann (1914) from South Australia, are in general agreement with each other and fall within the species described here as *T. australis*.

Etymology. This species is named after the location from which the sponge was first recorded.

Tethya popae sp. nov.
(Figs 8a, 12b, 26, 27, Plate 11a)

Type material. HOLOTYPE - AM Z5075: Cape Banks, New South Wales, Australia, $151^{\circ}15'E$, $34^{\circ}01'S$, intertidal, 21 September 1964.

Additional material. UAZA 9.9: Cape Banks, New South Wales, Australia, 151°15'E, 34°01'S, intertidal, 7 specimens, 21 September 1964.

Description. An irregular subspherical sponge 8 to 16mm in diameter (Fig. 26). The surface has ill defined low tubercles or is smooth. Oscules are apical, two to eight per sponge. Sponges occur singly or in tight clusters of two to six individuals connected by short broad basal stolons. The texture is firm, almost rubbery or waxy to the touch. The colour in life is bright deep orange (7.5R5/14). In ethanol the exterior is pompeian red (7.5R6/6 to 2.5YR7/6) and the exterior is pale pink (2.5YR7/4).

Skeleton. The sponge is easily compressible, a feature dictated by the small size of megascleres, the paucity of reinforcing microscleres and the presence of strong collagen depositions throughout the cortex and choanosome. The flexuous megasclere tracts are separated by plumose tracts of interstitial spicules throughout the choanosome (Fig. 27). The cortex is 750 to 1750µm deep. Megasclere tracts initially branch deep within the choanosome. Further branching within the cortex results in the formation of delicate tertiary fans just under the sponge surface. Micrasters and oxy-spherasters occur in extremely low density and are concentrated at the sponge surface and around subdermal canals, they are only occasional in the deeper cortex and in the choanosome.

Spicules. Megascleres: Small fine anisostrongyloxeas with proximal ends strongylote and distal ends fusiform oxeote, frequently stepped; 696(255-910) × 8(2-10)µm, n=10.

Microscleres: Megasters: Oxy-spherasters with small centurms; 32(20-55)µm, n=10. **Micrasters:** acanthochoiasters and acanthostrongylasters (Fig 8a); 11(7-13)µm, n=10; microoxyasters with irregular rays (Fig. 12b); 6(5-8)µm, n=10.

Ecology. The habitat is intertidal.

Remarks. *Tethya popae* is distinctive within the genus in having a low microscle-re content throughout the sponge and fine relatively short megascleres in strongly branching tracts. Interstitial spicules are present throughout the entire choanosome. *Tethya popae* is similar to *T. australis* in skeletal arrangement and oxy-spheraster morphology, but *T. popae* lacks oxyasters and a dermal micraster crust. The habit of the two sponges is also quite different: *T. australis* is large and solitary while *T. popae* is small and occurs in clusters of individuals connected by short basal stolons.

An undescribed species of *Tethya* from the west coast of New Zealand is similar to *T. popae*

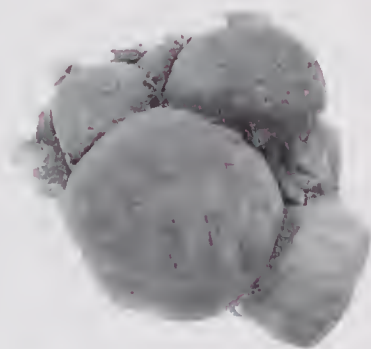
in skeletal arrangement and spiculation. The two species differ in gross morphology, colouration, and in details of spicule size, disposition and morphology. Additional material of the New Zealand species is required before a description of this new species can be made.

Etymology. The species is named after Miss E. Pope, Curator of sponges at the Australian Museum, Sydney, whose efforts on behalf of Australian marine invertebrate biology cannot be overestimated.

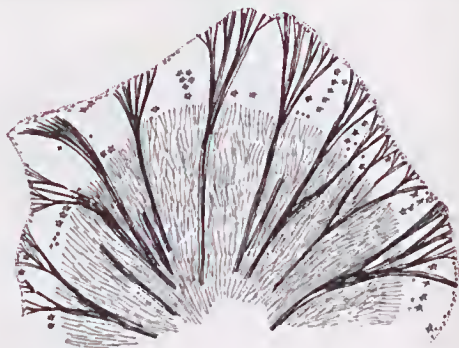
Tethya pellis sp. nov.
(Figs 5b, 9c, 7a, 28, 29)

Type material. HOLOTYPE-AM Z5077; Fairlight, Sydney Harbour, New South Wales, Australia, 151°13'E, 33°52'S, intertidal. 12 July 1960.

Description. A flattened, subspherical sponge, 40mm in diameter with surface divided into polygonal areas by pore grooves (Fig. 28). The texture is firm, resilient but compressible, smooth



26



27

Figs 26-27. *Tethya popae*: 26, preserved specimen, scale = 1 cm; 27, general skeletal arrangement.

and velvety to the touch. In ethanol the cortex is flesh-rose (10.0R7/2 to 6/2) and the choanosome brown-rose (5.0YR6/2 to 6/4).

Skeleton. Thick widely spaced megasclere tracts radiate through the choanosome into a collagenous cortex which is 7000 μm deep (Fig. 29). Within the upper third of the cortex megascleres fan to form wide delicate tertiary branches that terminate at the surface of the sponge. Micrasters form a very thin dermal crust and in the deeper cortex are found occasionally surrounding excurrent canals. Oxspherasters are common in the cortex. Choanosomal spicules include scattered oxyasters and micrasters.

Spicules. Megascleres: Anisostrongyloxeas, proximal ends strongylote, occasionally bent abruptly just below the end, distal ends hastate oxeote, stepped; 1300(250-2075) \times 3(12-30) μm , $n=10$.

Microscleres: Megasters: Oxspherasters; 64(25-120) μm , $n=20$. Oxyasters, unbranched with spined tips (Fig. 5b); 22(20-25) μm , $n=10$.

Micrasters: acanthochiasters (Fig. 9c), acanthotylasters (Fig. 7a), long-spined acanthooxyspherasters; 16(13-18) μm , $n=10$, microoxyasters; 8(5-11) μm , $n=10$.

Ecology. Solitary, shallow subtidal fringe down to 8m.

Remarks. *Tethya pellis* is comparable to *T. australis* and *T. popae* but differs in a number of points of general skeletal arrangement and morphology. *Tethya pellis* has no interstitial megascleres as do *T. australis* and *T. popae*, and oxspherasters are common throughout the entire width of the cortex rather than being restricted in distribution to the upper and lower regions of the cortex, as in *T. australis*. The choanosome of *T. pellis* contains only scattered micrasters and oxyasters, unlike *T. australis* which has all microsclere forms in abundance in the choanosome. In such general features as uniform oxspheraster distribution throughout the cortex, an absence of interstitial megascleres and the low microsclere density in the choanosome, *T. pellis* approaches *T. robusta*. The prominent diagnostic feature of *T. pellis* is the extremely thick cortex.

Etymology. The specific name is Latin for hide or skin and emphasises the strong cortical development of this species.

Tethya seychellensis (Wright)

(Figs 6c, 7b, 9a, 12a, 30, 31)

Alema seychellensis Wright, 1881:13.

Tethya seychellensis - Sollas 1888:427.

Donatia diploderma Burton, 1924:1039.

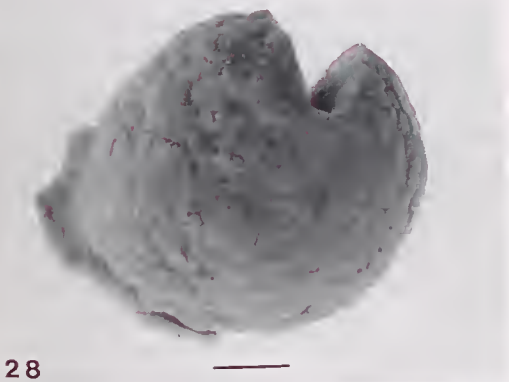
Tethya seychellensis - Hechtel 1965:65.

Tethya seychellensis - Bergquist 1969:68.

Tethya seychellensis - Bergquist *et al.* 1971:102.

Material examined. UAZA 11.115: Motupore Island, Papua New Guinea, 147°10'E, 9°30'S, 0.5-2.0m, 2 specimens, 20 December 1985; YPM 5283, YPM 5385, Port Royal, Jamaica, 76°51'W, 17°56'N, 24 July 1961; SUZS 3: Heron Island, Australia, 152°01'E, 23°27'S, intertidal, 1 specimen, 1 December 1962;

Description. A spherical sponge up to 25mm in diameter, adherent to the substrate by fine stolons (Fig. 30). The surface is smooth to microhispid with flattened polygonal or blunt narrow tubercles separated by deep pore grooves, or tessellated with buds arising on fine tissue filaments 5 to 10mm long. The texture is firm but compressible. Exterior colour in life is brown red (5.0R 4/6) and the interior is pale yellow. In ethanol the sponge is beige (2.5Y2/12) throughout.



28



29

Figs 28-29. *Tethya pellis*: 28, holotype, preserved specimen, scale = 1 cm; 29, general skeletal arrangement.

Skeleton. Megasclere tracts 250 to 500µm wide traverse the choanosome to radiate sharply in the cortex and form secondary branches with spicules protruding well beyond the sponge surface (Fig. 31). Dense brushes of interstitial megascleres radiate in a band in the outer choanosome. The cortex is one to two mm deep. Micrasters form a dense dermal layer on the sponge surface and are abundant subdermally. The central cortex is cavernous with dense aggregations of micrasters around canals. Oxyspherasters are occasional. Oxyspherasters and micrasters are densely packed in the lower cortex. Below this oxyspheraster band and extending to the inner boundary of the cortex is a collagenous layer up to 200µm thick which contains rare micrasters. A zone extending from the choanosomal periphery to a depth of 400µm is packed with smaller oxyspherasters and micrasters. Oxyasters and micrasters are extremely abundant throughout the choanosome and oxyspherasters are rare.

Spicules. **Megascleres:** Anisostrongyloxeas, proximal ends strongylote, distal ends hastate

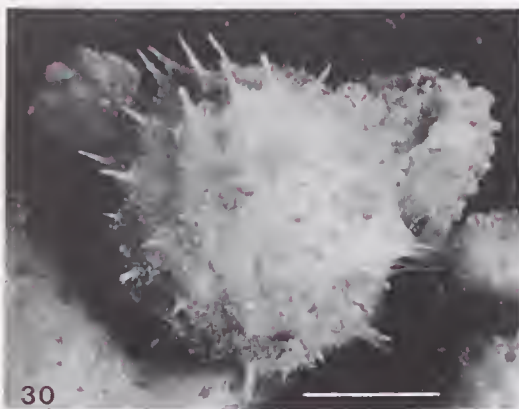
oxecote, stepped. Smaller spicules are flexuous, larger spicules frequently acutely curved below the proximal end; 1038(550-1500)×23(15-30)µm, n=30.

Microscleres: **Megasters:** Oxyspherasters, frequently with forked ray tips; 61(17-76)µm, n=20. Oxyasters with low number of curved rays and multiple terminal branching. The distal two thirds of each ray is lightly spined (Fig. 6c); 43(32-50)µm, n=10. **Micrasters:** acanthotylasters (Fig. 7b), acanthochiasters (Fig. 9a) and acanthostrongylasters; 12(7-13)µm, n=10; microoxyasters with fine smooth rays (Fig. 12a); 13(7-17)µm, n=10.

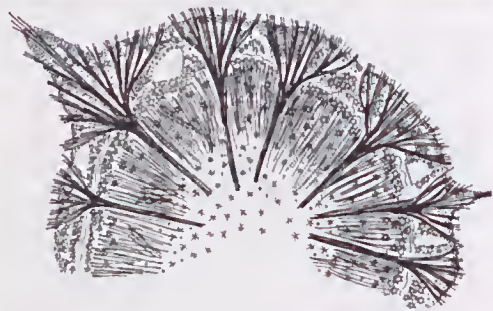
Ecology. Attached to the undersides of intertidal boulders and reef crest plate corals. In Papua New Guinea, sponges are only found on windward reefs while in Jamaica they are found on seagrass flats.

Remarks. The 'four layered cortex' described by Hechtel (1965) for Caribbean specimens of *Tethya seychellensis* is also present in Pacific specimens. There are small differences between Caribbean and Pacific *T. seychellensis*. Sponges from both Heron Island and Papua New Guinea have a greater density of choanosomal interstitial megasclere brushes than does *T. seychellensis* from Jamaica. Within the Pacific, Heron Island sponges have a slightly reduced spicule density throughout and individual spicules are finer. Specimens from Papua New Guinea have a compressed collagenous cortical band of approximately 200µm as opposed to Australian and Caribbean specimens where the corresponding region is 300 to 600µm wide. The basic skeletal arrangement is consistent in sponges from all three locations.

Tethya ingalli has sometimes been compared with *T. seychellensis* and even referred in synonymy to that species (Burton 1924). An obvious and major difference between *T. ingalli* (Holotype BMNH 77-5-21-140), and *T. seychellensis* is the degree of branching of the megasclere tracts; tract branching in *T. ingalli* is tertiary, it is secondary only in *T. seychellensis*. *Tethya seychellensis* also has a markedly lacunar cortex with microscleres predominantly in the outer and inner cortex while the cortex of *T. ingalli* is compact, oxyspheraster packed and collagenous throughout. The oxyaster morphology of *T. seychellensis* is quite distinct from the unbranched oxyasters in *T. ingalli*; the oxyasters of *T. seychellensis* are very characteristic with a small number of almost completely microspined rays with multiple terminal branching. Megascleres and microscleres of *T.*



30



31

Figs 30-31. *Tethya seychellensis*: 30, preserved specimen, scale = 0.5 cm; 31, general skeletal arrangement.

seychellensis are substantially different to those of *T. ingalli* in size and morphology.

Distribution. Tropical Atlantic coast of America, Indo-Pacific, Red Sea, Indian Ocean, Ceylon, Malaysia, Philippines, Tahiti, Australia.

Tethya coccinea sp. nov.
(Figs 2a, 8b, 32, 33)

Type material. HOLOTYPE-AM Z5082: Motupore Island, Papua New Guinea, 147°10'E, 9°30'S, 0.5-1.0m, 23 February 1985.

Additional material. UAZA 1148: Motupore Island, Papua New Guinea, 147°10'E, 9°30'S, 0.5-1.0m, 2 specimens, 2 January 1986.

Description. A solitary spherical sponge, 7 to 15mm in diameter, with thick flat basal attachment disc (Fig. 32). The surface is irregularly mammillate and hispid. Small oscules 0.5 to 1.0mm in diameter are scattered on the sides of the sponge. The texture is firm. The colour of the cortex in life is bright carmine (5R 5/12) and the choanosome is bright orange (2.5 YR 6/14). In ethanol the entire sponge is dull orange (5 YR 7/8). *Tethya coccinea* reproduces asexually through the production of external buds.

Skeleton. Large megasclere tracts form broad branched fans of secondary branches in the 2 to 3 mm wide cortex (Fig. 33). Loose brushes of smaller interstitial megascleres radiate in the upper periphery of the choanosome. Spicules protrude beyond the sponge surface. Micrasters form a narrow dense superficial dermal layer and are scattered subdermally. Micrasters are abundant throughout the choanosome. Large oxyspherasters are packed in the upper two thirds of the cortex while the cortical-choanosomal boundary is distinguished by a dense band of smaller oxyspherasters. Oxyspherasters attenuate in number into the choanosome. Oxyasters are abundant in choanosome.

Spicules. **Megascleres:** Anisostrongyloxeas, proximal ends strongylote, distal ends hastate oxeote, frequently stepped; 1505(350-1700) × 22(17-35)µm, n=30.

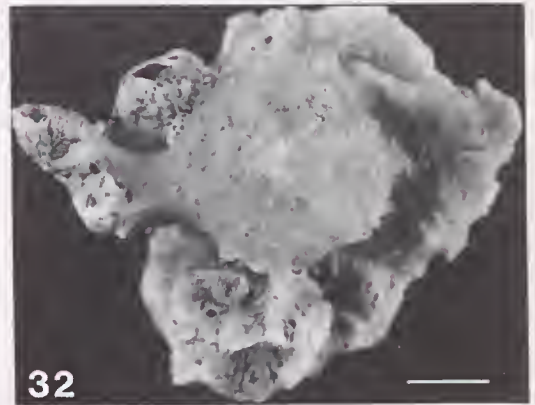
Microscleres: **Megasters:** Oxyspherasters (Fig. 2a); 89(20-110)µm, n=20. Ooxyasters, unbranched, with curved rays; 20(15-25)µm, n=20.

Micrasters: acanthochiasters, acanthooxyspherasters, acanthostrongylasters (Fig. 8b); 11(10-14)µm, n=11. microoxyasters with fine rays; 6(7-10)µm, n=5.

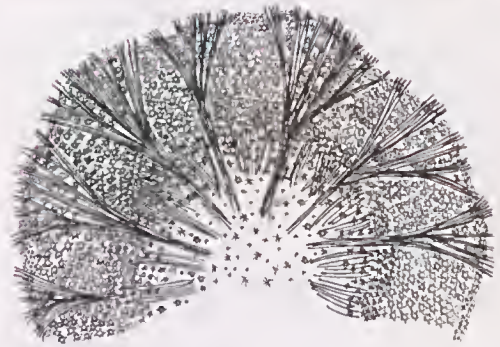
Ecology. Solitary, attached to the undersides of plate coral on windward reef crests.

Remarks. The closest species in the literature to *Tethya coccinea* is a specimen of *Tethya* from Bermuda that was not formally described but which was compared by Hechtel (1965) to *Tethya maza* Selenka. Examination of two specimens of *Tethya* sp. (cf. *maza*), YPM 5290 and YPM 5286, confirmed similarities in the general skeletal arrangement of the two species. *Tethya* sp. (cf. *maza*) has a dense surface micraster crust and a dense oxyspheraster packed cortex with robust megasclere tracts that fan in the cortex. Oxyspherasters, oxyasters and micrasters are abundant in the choanosome, as they are in *T. coccinea*.

Tethya coccinea and *T. sp.* (cf. *maza*) can be separated on the size and morphology of the spicules. The megascleres of *T. sp.* (cf. *maza*) are shorter (896(354-1225)µm), oxyspherasters smaller (15-82µm) and oxyasters smaller (14-18µm) than in *T. coccinea*. The morphology of the oxyspherasters also differs considerably between the two species; the oxyspherasters of *T. sp.* (cf. *maza*) have a small centrum and a low number of long robust rays while those of *T. coccinea* have



32



33

Figs 32-33. *Tethya coccinea*: 32, holotype, preserved specimen, scale = 0.5 cm; 33, general skeletal arrangement.

a large centrum and numerous small rays. The micrasters of *T. sp.* (cf. *maza*) are acanthostrongylasters.

Tethya coccinea exhibits a very distinctive differential colouration with carmine cortex and bright orange choanosome. De Laubenfels (1954:234) described *T. actinia* from Ebon Atoll in the West Central Pacific as having an identical colouration, a similar habitat and oxyasters of similar size. Examination of the specimen from Ebon Atoll (*T. actinia* USNM 22977) confirmed its identity to the holotype of *T. actinia* de Laubenfels (1950) from Bermuda. It is however very different from *T. coccinea* in skeletal arrangement, microscelere density, spicule size and morphology, and in colouration. *Tethya actinia* has slim megascelere tracts that fan only slightly in the thin cavernous cortex and interstitials are present throughout the choanosome. Oxspherasters and micrasters are moderately common but found only in the outer cortex of *T. actinia* whereas in *T. coccinea* these microscleres are densely packed throughout a solid collagenous cortex.

Tethya coccinea differs from *T. seychellensis* in cortical structure and in oxyaster morphology. These two species do, however, share secondary branched megascelere tracts, a palisade of interstitial spicules in the choanosome and megascleres with stepped distal ends.

Etymology. The species name emphasises the brilliance of the colour in life.

***Tethya robusta* Bowerbank**
(Fig. 34, Table 1)

Tethya robusta Bowerbank, 1872:10.

Donatia robusta - Burton 1924:1037.

Tethya robusta - Burton 1934:568.

Tethya robusta - Bergquist 1969:68.

Material examined. UAZA 11.30: Motupore Island, Papua New Guinea, 147°10'E, 9°30'S, 0.5-1m, 2 specimens, 18 June 1986; SUZS 1: Heron Island, Australia, 152°01'E, 23°27'S, intertidal, 1 specimen, 20 December 1962.

Description. A hemispherical sponge, up to 50mm in diameter, attached to the substrate by short broad basal stolons. The surface is microhispid and divided into polygonal areas 0.5 to 2.0mm wide, separated by shallow pore grooves. The texture is extremely firm to incompressible. The colour of the cortex in life and in ethanol is light yellow gray (5Y 8/2). The endosome is mustard yellow (2.5Y 7/8) in life.

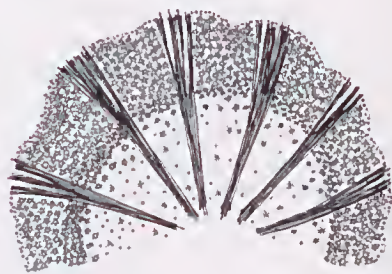
Skeleton. Slim compact megascelere tracts 230 to 580µm in diameter radiate through the choanosome, expanding slightly in the uniformly collagenous cortex to form secondary branches that terminate immediately below the surface. The choanosome lacks interstitial megascleres. Spicules project through the surface (Fig. 34). The cortex is 2 to 3 mm deep and packed with large oxspherasters. Micrasters are common on the sponge surface but do not form a dense layer. They are slightly less common in deeper regions of the cortex. Smaller oxspherasters than are in the cortex are present in variable numbers in the outer choanosome. Oxyasters and micrasters are scattered throughout the choanosome.

Spicules. Megascleres: Anisostrongyloxeas, proximal ends strongylote, hastate oxeote distally, spicules frequently curved to flexuous; 945(410-1850)×18(8-32)µm, n=20.

Microscleres: Megasters: Oxspherasters, larger in the cortex; 67(30-90)µm, n=20. Unbranched oxyasters, slender curved rays; 19(11-22)µm, n=20. **Micrasters:** acanthotylasters and acanthostrongylasters, rays frequently reduced to stumps; 10(7-12)µm, n=20; microoxyspherasters with thick centurms and irregular rays; 4(4-5)µm, n=10.

Ecology. *Tethya robusta* occurs singly or in groups of two and is found attached to the undersides of coral plates or boulders on shallow windward or leeward reef flats. At Motupore Island, this species is frequently found in close association with *Psammaphysilla purpurea* (Carter) and *Sigmadocia amboinensis* (Lévi).

Remarks. We regard *Tethya robusta* Bowerbank to be well described in the literature and an easily recognisable species, thus we have not compared our specimens with the holotype.



34

Fig. 34. General skeletal arrangement of *Tethya robusta*.

Table 1. Spiculation differences (μm) between specimens of *Tethya robusta* Bowerbank from Heron Island (Bergquist 1969) and Orpheus Island (Sarà 1990) on the Great Barrier Reef, Australia and from Motupore Island, Papua New Guinea (PNG). The range of spicule measurements are in parentheses and the mean precedes the range. Means are not available for Orpheus Island data.

Locality	Megascleres				Spherasters	Oxyasters	Micrasters
PNG	945	(410-1850)	x	18 (8-32)	67 (30-90)	19 (11-22)	10 (7-12)
Heron Island	1203	(447-2229)	x	20 (8-33)	78 (45-97)	19 (17-20)	11 (8-12)
Orpheus Island	-	(400-1600)	x	- (5-25)	- (30-90)	- (12-17)	- (9-12)

Specimens of *Tethya robusta* from Heron Island (Bergquist 1969) and Orpheus Island (Sarà 1990) are very close to those from Papua New Guinea in morphology and skeletal architecture. Papua New Guinea specimens have a lower overall microscle density with fewer oxyspherasters in the upper choanosome, a dermal micraster crust that is almost non existent and micrasters and oxyasters that are only sparse and scattered in the choanosome. The megasccleres of Heron Island specimens are substantially larger than those of other specimens (Table 1).

Tethya robusta has been compared with *T. ingalli* and several times synonymised with this species (e.g. Dendy 1916). Although both of these species have a dense oxyspheraster packed cortex, *T. ingalli* is easily distinguished from *T. robusta* in having elaborate tertiary megascclere tract branching, interstitial megasccleres in the choanosome and larger oxyspherasters and oxyasters.

Distribution. Australia, Solomon Islands, Indian Ocean, Red Sea.

Tethya sollasi sp. nov.
(Figs 2c, 35, 36)

Type material. HOLOTYPE - AM Z5084: Isle M'Ba, New Caledonia, 165°30'E, 21°30'S, intertidal, 24 April 1989.

Additional material. UAZA 9.6: Isle M'ba, New Caledonia, 165°30'E, 21°30'S, intertidal, 3 specimens, 24 April 1989.

Description. A solitary, spherical to subspherical sponge, 5 to 18mm in diameter or flattened and elongate when two to three sponges are confluent (Fig. 35). Sponges are attached basally to the substrate by a narrow skirt of tissue emanating from the base of sponge. The surface is marked by low polygonal to inverted cone shaped tuberculae, 1.4 to 2.5mm wide, separated by deep pore grooves. Oscules are apical and the texture is incompressible, rough to the touch. The colour in life of the exterior is rose (2.5R7/6 to 6/

8) and the interior yellow white (5.0Y9/4). In ethanol the sponge is cream (2.5Y8/3). This species reproduces by budding, buds frequently becoming confluent with the parent sponge.

Skeleton. Narrow megascclere tracts 318 to 490 μm wide radiate abruptly in the cortex to form secondary branches that terminate at the surface and support the surface tubercles (Fig. 36). Interstitial megasccleres are abundant throughout the choanosome and arc radiate to confused in orientation. The cortex is extremely lacunar, heavily collagenous throughout and 2 to 4 mm deep. Micrasters are abundant in a dermal layer and are scattered below this in the cortex and choanosome. Large oxyspherasters pack the cortex while smaller oxyspherasters are abundant in the choanosome. The cortex is differentiated from the choanosome by a marked increase in oxyspheraster density on the cortex-choanosomal boundary.

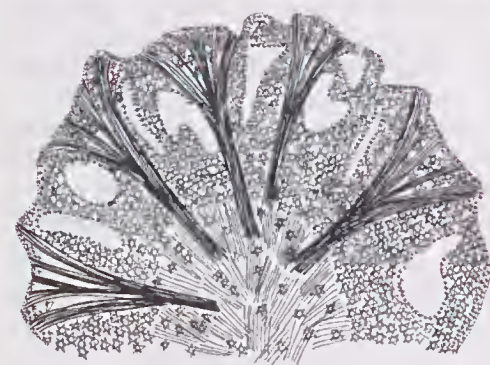
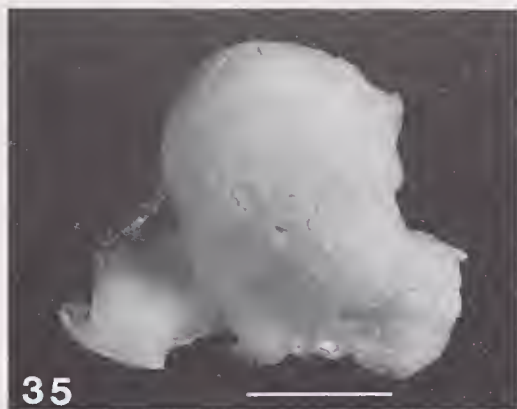
Spicules. Megasccleres: Anisostrongyloxeas, proximal end strongylote, distal end hastate or fusiform oxete, stepped; 965(343-1960)x21(13-31) μm , n=20.

Microsccleres: Megasters: Oxyspherasters (Fig. 2c). The smallest oxyspherasters are occasionally mammillate or concave; 49(12-75) μm , n=20.

Micrasters: acanthooxyspherasters, acanthostongylasters, acanthotylasters and acanthochiasters with developed centurms; 13(10-15) μm , n=20; microoxyasters; 5(3-8) μm , n=10, microoxyspherasters with mammillate rays; 5(3-8) μm , n=5.

Ecology. Found under plate coral rubble on intertidal inshore reef flats.

Remarks. *Tethya sollasi* is distinctive within *Tethya* in combining an extremely cavernous cortex that is packed with oxyspherasters, megascclere tracts that radiate abruptly and form secondary branches in the cortex, and abundant oxyspherasters and interstitial megasccleres throughout the choanosome. In a number of these features *T. sollasi* is very similar to *T. coccinea*, particularly in the morphology of the cortical megascclere fans, in the possession of a



Figs 35-36. *Tethya sollasi*: 35, holotype, preserved specimen, scale = 1 cm; 36, general skeletal arrangement.

oxyspheraster packed cortex, in having a cortex-choanosomal boundary that is packed with oxyspherasters, and a choanosome with abundant oxyspherasters which are smaller than those in the cortex, and which attenuate in number within the choanosome. The major features of *T. sollasi* that separate it from *T. coccinea* are an absence of oxyasters, larger megascleres, microoxyspherasters in the micraster complement, and interstitial megascleres throughout the choanosome. *Tethya coccinea* also has much larger oxyspherasters than does *T. sollasi*.

Tethya australis, *T. popae*, *T. pellis*, *T. seychellensis*, *T. coccinea* and *T. sollasi* all have a generally similar skeletal arrangement with broadly radiating branching megasclere tracts, pink cortical pigmentation, stepped megascleres and acanthochiasters in the microscclere complement. Oxyasters are present in all except *T. sollasi* and *T. popae*. Within this group there are differences in the degree of megasclere tract branching and in spicule densities; *T. australis*, *T. popae*, and *T. pellis* have low microscclere density and

exhibit tertiary branching of flexuous megasclere tracts. *Tethya seychellensis*, *T. coccinea*, and *T. sollasi* have high spicule density particularly in the cortex and have only secondary megasclere tract branches.

Etymology. The species is named after W.J. Sollas who authored the *Challenger* volume on the old order Tetractinellida.

Tethya fastigata sp. nov.

(Figs 6a, 7c, 9b, 37-39, Plate IIb)

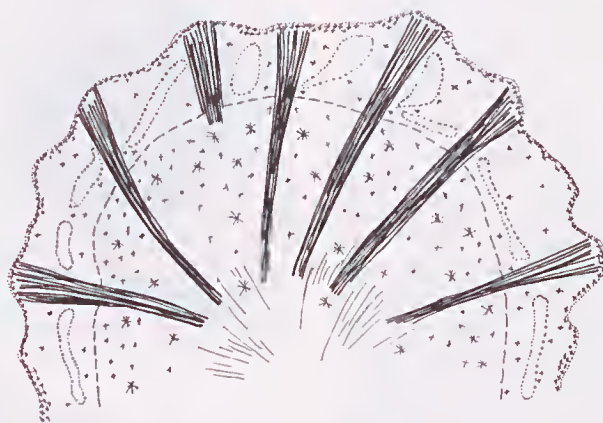
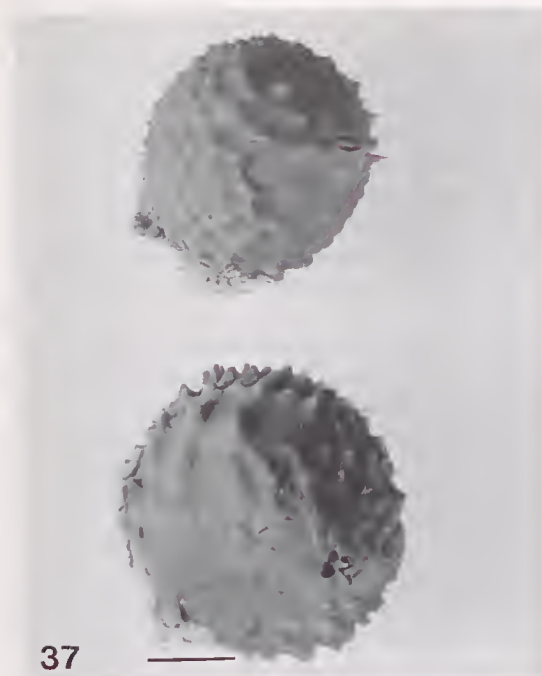
Type material. HOLOTYPE - AM Z5078: Poor Knights Islands, New Zealand, 174°44'E, 35°29'S, 30m, 22 November 1974.

Additional material. UAZA 9.12: Poor Knights Islands, 174°44'E, 35°29'S, 30m, 5 specimens, 22 November 1974; UAZA 5: Hcn Island, 174°42'E, 35°53'S, 40m, 1 specimen, 15 February 1967; UAZA E267: Alderman Islands, 176°05'E, 36°58'S, 25m, 1 specimen, 16 April 1967; UAZA 6.28: Cape Brett, 151°15'E, 34°01'S, 12-24m, 5 specimens, 15 December 1988; UAZA 30: Cavalli Islands, 173°56'E, 34°59'S, 18m, 1 specimen, 15 December 1988.

Description. A solitary ovoid sponge, 40 to 60mm in diameter, always with one to three large raised apical oscules (Fig. 37, Pl. IIb) and attached to the substrate by short thick stolons. The surface is coarsely conulose and the conules are blunt and regularly spaced. In life the surface appears as a delicate lattice in which cellular tracts stretch between conules (Pl. IIb). The texture is barely compressible but fleshy to touch. The colour of the cortex in life is bright orange (2.5YR 6/10 to 6/14), orange (7.5YR 7/10), or brick red (7.5R 5/12), the choanosome is always yellow brown (2.5YR 6/10). In ethanol 2.5Y8/4 to 7/4. *Tethya fastigata* reproduces asexually by the production of internalised buds.

Skeleton. Widely separated fine megasclere tracts 275 to 539µm in diameter radiate slightly toward the surface and terminate below it (Fig. 38). Interstitial megascleres occur in the inner choanosome. The cortex is uniformly extremely collagenous, 1000 to 4000µm deep, and lacunar. Micrasters form a discontinuous dermal layer one to two spicules deep at the surface, and within the cortex are uncommon below this level. Micrasters and oxyasters are abundant in the choanosome but micrasters decrease in density towards centre.

Spicules. Megascleres: Anisostrongyloxeas, frequently gently curved, proximal ends strongylote, distal ends fusiform oxecote, stepped: 1969(990-2425) × 21(7-35)µm, n=20.



38

Figs 37-39. *Tethya fastigata*: 37, preserved specimen, scale = 1 cm; 38, general skeletal arrangement; 39, deformed micrasters.

Microscleres: Megasters: Oxyasters, regular with smooth unbranched curved rays or irregular with rays that split in the lower third, frequently of different lengths and often bulbous at the ray base (Fig. 6a); 29(18-39) μm , $n=20$. **Micrasters:** acanthotylasters (Fig. 7c) and acanthochiasters (Fig. 9b), predominantly highly deformed to diacts, triacts and quadractinal spicules, often with double or triple headed ray tips, frequently with great ray and centrum thickness, large size range (Fig. 39); 14(9-20) μm , $n=20$; acanthooxyspherasters;

10(8-14) μm , $n=20$; microoxyasters; 6(2-9) μm , $n=10$; microoxyspherasters; 7(5-8) μm , $n=10$.

Ecology. Always solitary and occurring on light exposed bare rock surfaces.

Remarks. *Tethya fastigata*, with the later described *T. amplexa*, is distinct within the genus in lacking oxyspherasters. It also has micrasters that are predominantly deformed multiactinal spicules with multiple headed ray tips (Fig. 39). *Tethya fastigata* has a conulose surface which is also unusual in *Tethya* species.

Etymology. The species name emphasises the conulose surface morphology.

***Tethya amplexa* sp. nov.**
(Figs 6b, 40-41)

Type material. HOLOTYPE - AM Z5081: Mimiwhangata, northern New Zealand, 174°27'E, 35°26'S, 7m, 20 July 1974.

Additional material. UAZA 14: Mimiwhangata, 174°27'E, 35°26'S, 7m, 5 specimens, 20 July 1974; UAZA 9.1, 8 February 1967, UAZA 9.3, 26 June 1974; Cape Karikari, 173°24'E, 34°47'S, 5m, 2 specimens; UAZA 4: Hahci, 175°48'E, 36°51'S, 3-5m, 1 specimen, 14 March 1974; UAZA 3: Great Barrier Island, 175°24'E, 36°13'S, 5m, 1 specimen, 14 March 1974; UAZA 40: Mercury Islands, 175°52'E, 36°38'S, 3-10m, 2 specimens, 4 December 1988; UAZA 50: Cape Brett, 174°20'E, 35°10'S, 22m, 3 specimens, 12 December 1988; UAZA 69: Bay of Islands, 174°15'E, 35°13'S, 12m, 1 specimen, 14 December 1988; UAZA 61: Cavalli Islands, 173°56'E, 34°59'S, 20m, 1 specimen, 12 December 1988; UAZA 9.2: Alderman Islands, 176°05'E, 36°58'S, 6m, 1 specimen, 3 April 1987; UAZA 6.31: Ohinau Island, Mercury Islands, 175°52'E, 36°44'S, 10m, 2 specimens, 6 December 1988.

Description. A spherical to subspherical sponge, 30 to 70mm diameter in life with the surface completely encrusted with polyzoans, calcareous algae, polychaetes, shell fragments and gravel (Fig. 40). Sponges on a semi-mobile substrate are attached by a long curved flexible peduncle 25 to 40mm long and 7mm wide. Oscules, where visible, are apical, raised and 3 to 5 mm in diameter. Broad flat tubercules 2 to 4 mm wide and high cover the sponge surface. The texture is compressible, yet resilient in life. The exterior colour in life is yellow (2.5 Y 8/10), the interior yellow brown (7.5 YR 5/8 to 7/8), in ethanol 2.5Y8/4. *Tethya amplexa* reproduces by the production of internalised buds.

Skeleton. Abundant robust megasclere tracts 440 to 800µm wide traverse the cortex with only a slight divergence in the upper cortex to produce an occasional branch (Fig. 41). Spicules protrude just beyond the sponge surface. Megasclere tracts raise the surface into broad low tubercules to which encrusting organisms attach. Interstitial megascleres radiate in brushes in the inner choanosome. The cortex is lacunar, variable in thickness, 1 to 3 mm deep and packed with pigmented granules and detritus. Both the cortex

and choanosome are strongly collagenous. Micrasters form a dense dermal layer 50 to 100µm deep and are abundant throughout the cortex. In the outer choanosome micrasters are abundant to 800µm deep, below this they are rare. Oxyasters are abundant throughout the choanosome.

Spicules. Megascleres: Anisostrongyloxcas proximal ends narrow strongly, distal ends abrupt hastate oxecote, occasionally fusiform oxecote, often stepped; 1645(318-2327) × 24(15-32)µm, n=20.

Microscleres: Megasters: Oxyasters with acutely bent, thick, occasionally split rays (Fig. 6b) with spined tips; 23(16-35)µm, n=20. **Micrasters:** acanthotylasters, acanthochiasters and acanthooxyspherasters, occasionally deformed into diacts or triacts with thickened rays and centurms; 18(10-20)µm, n=20; microoxyasters; 7(5-8)µm, n=10; microoxyspherasters; 8(6-8)µm, n=20.

Ecology. *Tethya amplexa* occurs individually on bare rock faces in deeper water or almost



Figs 40-41. *Tethya amplexa*: 40, preserved specimen, scale = 1 cm; 41, general skeletal arrangement.

obscured among turfing algae in the shallow subtidal.

Remarks. In spicule complement, disposition and dimensions, and in skeletal architecture, *Tethya amplexa* and *T. fastigata* are very similar. Both species lack oxyspherasters, both contain oxyasters, and have megasclere tracts that barely branch. They differ considerably, however in their ecological characteristics and in gross morphology. *Tethya amplexa* occurs from 3m to 22m whilst *T. fastigata* occurs from 12m to 90m. *Tethya amplexa* is subspherical and always covered with epizootic organisms which obscure broad surface tuberculae and protruding megascleres. In *T. fastigata* the surface is smooth, clear of encrusters and markedly conulose with raised apical oscules.

There are differences in spiculation between the two species: *Tethya amplexa* has a proportionately greater spicule density in all regions of the cortex and choanosome than does *T. fastigata*, although the disposition of the spicules in these regions is the same for both species. The frequency of deformity in the micrasters of *T. fastigata* is much greater than in the micrasters of *T. amplexa*.

Tethya amplexa and *T. fastigata* constitute a unique group within *Tethya* that lacks oxyspherasters and has deformed micrasters. These micrasters are reminiscent of the polyrhabs of *Tethyorrhaphis* and the recognition of these two very novel species of *Tethya* permits a reevaluation of the status of the former genus.

Etymology. The species name refers to the crust of epizootic organisms that are associated with specimens of *Tethya amplexa*.

Tethya communis sp. nov.
(Figs 2b, 5a, 13-14, 42-43)

Type material. HOLOTYPE - AM Z5087: Cape Banks, New South Wales, Australia, 151°15'E, 34°01'S, intertidal, 13 December 1960.

Additional material. UAZA 9.10: Cape Banks, New South Wales, 151°15'E, 34°01'S intertidal, 4 specimens, 13 December 1960.

Description. A spherical to subspherical sponge, 7 to 12mm diameter, growing in clumps in which individuals are fused laterally to form a dense mat 5 to 25mm thick (Fig. 42). The surface is mammillate, microscopically smooth and waxy to the touch. Oscules are few and are apical. The texture is firm. The colour of the cortex in ethanol is dull grey pink (7.5R 7/4) and the choanosome is reddish yellow (2.5 YR 6/4).

Skeleton. Fine flexuous megasclere tracts 125 to 300µm wide spread to form delicate tertiary branches in the upper half of a collagenous cortex 1 to 2 mm deep (Fig. 43) and terminate at the surface. Loose brushes of interstitial megascleres fan radially throughout the choanosome. Oxyspherasters are extremely rare in the cortex. Polyrhabs form a moderately dense layer at the surface and are uncommon below this in both the cortex and choanosome. Micrasters are uncommon throughout the sponge. Oxyasters are uncommon in the choanosome.

Spicules. Megascleres: Curved anisostrongyloxeas that are occasionally stepped, proximal end strongylote, distal end fusiform to hastate stylote, isostrongyloxeas common; 960(290 to 1225) × 9(5-12)µm, n=20.

Microscleres: Megasters: Oxyspherasters (Fig. 2b) with stout long rays, frequently deformed with several shortened strongylote rays per spicule; 46(38-55)µm, n=5. Oxyasters (Fig. 5a), frequently plesiaster-like in form; 10(7-12)µm, n=10. **Micrasters:** acanthotylasters and acanthooxyspherasters, frequently with rays of different lengths and often entirely microspined; 13µm, n=10; Polyrhabs (Figs 13, 14); 10(7-13)µm, n=20.

Ecology. Intertidal.

Remarks. *Tethya communis* is distinct in having polyrhabs that form a crust on the sponge surface, isostrongyloxeas in the megasclere complement, oxyspherasters, oxyasters and micrasters that are frequently deformed, and a paucity of microscleres generally.

Lendenfeld (1888) established the genus *Tethyorrhaphis* for tethyid species that contained polyrhabs in a surface crust. Five species of *Tethyorrhaphis* were described by Lendenfeld (1888) all of which were referred to *T. laevis* by Hallmann (1914). The recent discovery of *Tethya communis* which also possesses polyrhabs has necessitated consideration of the status of the genus *Tethyorrhaphis*. We are now able to do this on the basis of having a more detailed knowledge of the range of morphologies within *Tethya*.

Tethya communis is very close to *T. popae* in details of general skeletal arrangement. These two species have flexuous megasclere tracts that branch in the cortex to form delicate tertiary fans and interstitial megascleres that are present throughout the choanosome. These features are also found in *T. australis*. Both *T. popae* and *T. communis* also have a paucity of microscleres. These two species are separated by the presence

of polyrhabds, isostrongyloxeas and frequent deformation of the microscleres in *T. communis*.

Tethya fastigata and *T. amplexa* have deformed micrasters which are also predominantly confined to a surface crust as in species previously referred to *Tethyorrhaphis*. The distinction is fine between the morphology of these dermal micrasters and in all three species the dermal spicules have a reduced ray number and multiple terminal heads. The polyrhabds of *T. communis* are completely microspined whilst the spination of micrasters of *T. fastigata* and *T. amplexa* is always terminal on the rays. *Tethya fastigata* and *T. amplexa* also have few microscleres generally, and they lack oxyaspherasters. The latter are rare in *Tethya communis*.

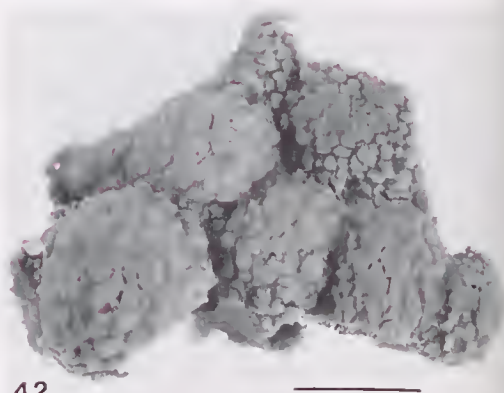
Examination of a specimen of *Tethyorrhaphis laevis* Lendenfeld (BMNH 86.8.27.529) confirmed that this species also has the general skeletal features of *Tethya*. It has cortical oxyaspherasters, tertiary branching of megasclere tracts in the cortex, a dermal spicule crust of polyrhabds, oxyasters in the choanosome and moderately common microscleres in the cortex and in the choanosome. *Tethya communis* differs from *Tethyorrhaphis laevis* Lendenfeld in having very few microscleres; those of *Tethyorrhaphis laevis* are more abundant and larger, the latter species also lacks interstitial spicules.

In *Tethyorrhaphis laevis* and *Tethya communis*, oxyasters are only slightly bigger than micrasters, and are frequently plesiaster-like with irregular rays emanating from an elongate axis, not from a centrum. The micraster component of these two species and of *Tethyorrhaphis oxyaster* Burton (BMNH 30.8.15.30) consists only of acanthotylasters and acanthooxyspherasters. Microoxyasters or microoxyspherasters are absent in all three species. Isostrongyloxeas are present in *Tethyorrhaphis laevis*, *Tethyorrhaphis oxyaster* and *Tethya communis*. The differences found between species formerly put in *Tethyorrhaphis* and *Tethya* are small and none emerge as strong discriminating characters in our phylogenetic analysis (Fig. 44). They function as useful species descriptors. Consequently we have relegated *Tethyorrhaphis* into synonymy with *Tethya* and all described species are referred to that genus. We can confirm *Tethya laevis* and *Tethya oxyaster* as distinct species, the status of others can only be determined by collection of further material.

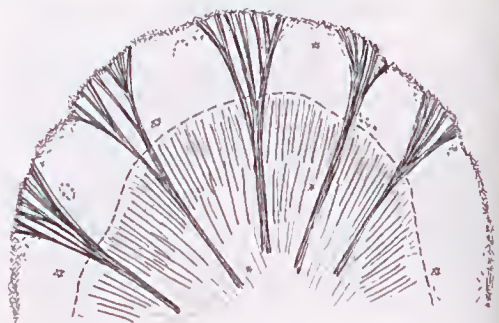
Etymology. The species name describes the way that these sponges, by lateral fusion of adjacent cortices, form a communal mat.

DISCUSSION

Early attempts to revise the genus *Tethya* (Topsent 1918; Burton 1924) have concentrated on a small number of characters—specifically spicule category, whether present or absent and spicule morphology—and these characters have been treated independently and given differing emphases. More recently Sarà (1987) has advocated using a broader descriptive base and this also has been our intention over the period this paper has been in preparation. Sarà (1987) listed only fourteen valid species of *Tethya*. He noted that many more species await description and certainly we are aware of further species from the Central and East Pacific and from Australasia for which additional material is required before description. The 11 new and 3 other species described in this report widen the spectrum of morphologies known within the genus *Tethya* and draw attention to a number of characters which have not been emphasized previously in species descriptions.



42



43

Figs 42-43. *Tethya communis*: 42, holotype, preserved specimen, scale = 1 cm; 43, general skeletal arrangement.

The megascleres in *Tethya* are simple and uniform and as structural spicules their arrangement dictates the form of the sponge. In general terms this basic arrangement is invariable with major tracts radiating from a central basal core through choanosome and cortex to terminate at, or beyond the surface in protrusions between which pores lie in grooves. A consequence of this uniformity in megasclere structure and general arrangement has been that most authors have disregarded the detail of megasclere arrangement and have concentrated primarily on microsclere morphology and occasionally on microsclere localization when differentiating between species.

We have found that cortical and choanosomal megasclere arrangement varies within the genus and that there are several distinct patterns represented in the group of species we have reported on. Within a species the particular arrangement of megascleres is consistent. In the cortex, megasclere tracts are either of uniform diameter throughout or are radiating. Radiating megasclere tracts can express secondary or tertiary branching. Tracts can also be sinuous or strictly radial in orientation. In the choanosome, interstitial megascleres can form a peripheral palisade, be basally situated, present throughout or completely absent from the region. Similar attention to detail of structural skeletal pattern has already proved invaluable in differentiating species of *Polymastia* (Boury-Esnault 1987).

In addition to arrangement of the megascleres, their morphology provides additional diagnostic characters; the distal extremity of the spicule can be stepped or non-stepped and is either hastate or fusiform oxeote. Spicules with hastate or fusiform oxeote distal ends can both be present in the megasclere complement of any one species. Megascleres are straight, curved or flexuous.

We have found that the presence or absence of various categories of microscleres, their morphology, and the density and disposition of these spicules within various regions of the sponge are informative characters for defining species. For oxyspherasters the regional differentiation of spicule size is noteworthy, and for both oxyspherasters and oxyasters, the size differences in these spicules can be marked between species.

The small size of the micrasters makes the detail of their ray structure difficult to resolve accurately. We have found the use of scanning electron microscopy in conjunction with light microscopy to be helpful in defining and differentiating these spicules. It would be useful to verify older descriptions which differentiate micraster

categories in this way. Deformity in micrasters and the presence or absence of a micraster crust on the surface of the sponge provide additional descriptive characters.

Features of the gross tissue morphology also provide diagnostic characters: the cortex is either solid or lacunar, collagen aggregation within the region can be limited to a basal layer, or be marked throughout. In some species there is strong collagen deposition in the choanosome as well. The relative width of the cortex in relation to the sponge radius and the structure of the boundary between cortex and choanosome also vary from species to species. Superficial and choanosomal pigmentation is a stable specific character and can be utilised in descriptions.

In addition to aspects of aspects of spiculation and structure, the species of *Tethya* described here occupy a range of ecological habitats and exhibit several different methods of asexual reproduction, either producing external stalked buds, budding from basal stolonal extensions or producing internalised buds. These features need to be recorded for a greater range of species but patterns of growth whether solitary, aggregated or basally fused, and methods of asexual reproduction are consistent within species.

To make a sensible appraisal of the genus *Tethya* requires that a full descriptions be available for as many species as possible across the geographic range of the genus. At present this information is not available. The importance of having a wide geographic coverage of species is well illustrated by the discovery of the closely related New Zealand species *T. amplexa* and *T. fastigata*. Both species lack oxyspherasters, have a simple arrangement of spicule tracts, basal interstitial megascleres and deformed micrasters. In this latter feature *T. fastigata* and *T. amplexa* are close to species previously assigned to the genus *Tethyorrhaphis* known only from southern Australia. The morphology represented by these two New Zealand species is not found in any *Tethya* species described from other locations and permits us to evaluate the status of the genus *Tethyorrhaphis* and to incorporate it within *Tethya*.

Structural and spicule characters such as those used in present descriptions need also to be determined accurately for some older species such as *Tethya deformis*, *T. japonica* and *T. peracnata* by reference to type material and new collections. Such information in conjunction with this paper will provide a framework within which new species can be recognized and older names applied more precisely. At present the tendency for

Table 2. Characters and character states of *Tethya*. ¹Tethyid character states do not apply to the outgroups, as *Aiptos* sp. and *Suberites* sp. do not possess a defined cortex therefore outgroups are coded as absent. ²Tethyid character states do not apply to the outgroup as *Aiptos* sp. and *Suberites* sp. do not have stronglyloxeas, therefore outgroups were coded as absent. ³Character states are unique to the species listed. ⁴Ranked maxima for spicule measurements per species in characters 14 and 22 and cortex and body diameter measurements in characters 6 and 31 respectively were plotted against the corresponding species name. Separate clusters of data points were then designated as character states. Character states in characters 14, 22 and 31 are presented as a single maximum diameter, or a range of maximum diameters. ⁵Only the measurements of specimens examined were used to form character states for character 31, as references to the size of *Tethya* specimens in the literature are often lacking and species designation is dubious.

1. Cortex ¹ a. lacunar b. solid c. absent	11. Strongyloxea distal morphology ² a. hastate oxeote b. fusiform oxeote c. a and b d. strongyloxeas absent	23. Dermal micraster crust a. present b. scarce c. absent
2. Collagen distribution a. basal collagenous layer in cortex b. collagen throughout cortex c. collagen in cortex and choanosome d. collagen scarce	12. Megasclere extremity a. stepped b. non-stepped	24. Acanthostongylasters a. present b. absent
3. Cortex-choanosomal boundary ¹ a. scalloped b. irregular scalloping c. linear d. absent	13. Megasclere profile a. curved b. flexuous - <i>Tethya robusta</i> ³ c. straight	25. Acanthotylasters a. present b. absent
4. Microscle density in choanosome a. dense b. common c. rare d. absent	14. Oxspherasters ⁴ a. 110-120mm b. 67-82mm c. 52-55mm d. absent	26. Acanthooxyspherasters a. present b. absent
5. Microscle density in cortex ¹ a. packed b. common c. rare d. absent	15. Disposition of oxyspherasters in cortex a. present throughout b. present predominantly in upper to middle cortex c. absent d. present in upper and lower cortex - <i>Tethya seychellensis</i> ³	27. Acanthochiasters a. present h. absent
6. Mean cortex width relative to the sponge radius ⁴ a. 24.5-40% b. 13.6-22% c. 8-9.6% d. cortex absent	16. Oxspheraster size in choanosome a. present and same size as in cortex b. present and smaller than in cortex c. absent	28. Microoxyasters a. present b. absent
7. Form of megasclele tracts a. robust b. sinuous	17. Additional choanosomal oxyspherasters a. present b. absent	29. Microoxyspherasters a. present h. absent
8. Development of megasclele tracts in cortex a. non-fanned b. fanned unbranched c. fanned with secondary branch d. fanned with tertiary branch	18. Mammillate oxyspherasters a. present b. absent	30. Deformity of microscleres a. deformity to diacts, triacts and multiheads h. reduction in rays to stumps c. centrum development d. absent
9. Megascleles at sponge surface a. protrude well beyond surface b. occasional spicules just protrude c. flush with surface	19. Concave oxyspherasters a. present h. absent	31. Sponge dimensions ^{4,5} a. 40-59cm b. 25cm c. 11-18cm
10. Interstitial choanosomal spicules a. peripheral palisade b. throughout c. basal d. absent e. scattered with loose radial orientation	20. Cortical conical long-rayed oxyspherasters ¹ a. present b. absent	32. Surface colouration in life a. pale yellow, buff, cream b. bright orange - <i>Tethya aurantium</i> ³ c. orange, brown, yellow d. pink red - colour retained in alcohol e. pink red - colour lost in alcohol f. bright deep orange - <i>Tethya popae</i> ³
	21. Cortical conical short-rayed oxyspherasters ¹ a. present b. absent	33. Ecological habitat a. Deep water - <i>Tethya bullae</i> ⁴ h. intertidal to shallow subtidal c. a and h
	22. Oxyasters ⁴ a. 11mm - <i>Tethya communis</i> ³ b. 20-25mm c. 31-40mm d. 50mm terminally branched - <i>Tethya seychellensis</i> ³ e. absent	34. Asexual reproductive mode a. budding with long basal stolons where individuals remain attached but are independent b. budding with short basal stolons where individuals remain in confluent groups c. filament budding leading to solitary individuals d. Internal buds leading to solitary individuals e. gemmules - <i>Aiptos</i> sp. <i>Suberites</i> sp. ⁴

most authors is to lump many species under one name on the basis of individual aspects of spicule complement thus creating an impression that *Tethya* is a genus of widespread hypervariable species. Our studies suggest rather that there are many quite locally distributed morphologically and biochemically distinct species.

It will be useful in future revisionary work to employ strictly consistent terminology and groups

of characters that are descriptive of the regions of the sponge. In the cortex for example, all attributes which permit that region to function are interrelated, and thus it can be argued that it is the combination of features which is the informational unit, not the individual components.

Phylogenetic considerations: An objective for Sarà (1987) and in this study of *Tethya*, is to determine whether subdivision of the genus into

a number of genera or subgenera can be supported. Through a close appraisal of morphological data from species discussed here, we have found that particular sets of characters and character states do indeed divide the genus into groups of species.

An exploratory phylogenetic analysis using morphological characters was carried out to detect whether subgroups could be recognised within the Southwest Pacific species of *Tethya*. The phylogenetic analysis was carried out using PAUP Version 2.4 (Swofford 1985). The data was unordered and the global branch swapping option was used to ensure retrieval of all minimum length trees. Plesiomorphies for the ingroup *Tethya* plus the outgroup are listed in Table 4.

The characters and character states of *Tethya* identified during descriptions of the species are listed in a character-taxon matrix in Table 2. For certain characters some taxa may not logically possess the given states, for example, the possession of a histologically-defined cortex and possession of asters in the suberitid outgroups. In such cases these characters states have been coded "absent" instead of unknown, otherwise indicated by "?". When a state is coded as unknown, parsimony analysis assumes that any of the other states can take its place. It can be shown that this artificially reduces the length of the phylogenetic tree (A. Rodrigo pers. comm. 1991).

Before a formal phylogenetic analysis was conducted, all characters (Table 2) were categorised as either *well defined* or *questionable*. *Well defined* characters are those for which the character states can be easily assigned, and *questionable* characters are those for which there is a possibility of ambiguity in their assignment of character states. This *a priori* categorisation of characters

provides a qualitative confidence value for the subsequent phylogenetic analysis (Rodrigo 1990). If the most consistent characters in the analysis, or the characters that primarily determine the tree topology, were coded *a priori* as *well defined*, then we can feel confident that the topology of the tree is not based on characters that have a high risk of miscoding, i.e., *questionable* characters.

As a high number of parallelisms and reversals were postulated in the initial phylogenetic tree, character weighting was considered to be appropriate (Farris 1969). Each character was thus weighted using a successive approximation weighting procedure (Farris 1969) (Table 4). After the first weighted analysis, characters remained stable on the tree. Confidence in the computer-generated Successive Approximation weights (Farris 1969), given in Table 4, was increased, as the sum of the weights assigned to *well defined* characters was greater (199.714) than that assigned to *questionable* characters (54.030).

Aptos sp. and *Suberites* sp. (Order Hadromerida, Family Suberitidae) were used as outgroups. These Suberitidae were chosen as an outgroup in preference to other aster-bearing Hadromerida, such as the Spirastrellidae and Clionidae, as these Hadromerida differ vastly in all major morphological features from the Tethyidae, and the Tineidae are only questionably hadromerid. The most appropriate group against which to assess the status of the Tethyidae is the one chosen. This is supported by molecular data (Kelly-Borges *et al.* 1990) and secondary metabolite data (Bergquist *et al.* 1991).

We have used two outgroups in the phylogenetic analysis. An unrooted tree containing only one outgroup can always be rooted so that the ingroup

Table 3. Character state matrix for *Tethya*. Characters and states are listed in Table 2. Asterisks indicate species used as outgroups. When a character state is unknown for a particular species, the character is coded with a question mark.

Species	Character 1-34																																			
<i>Tethya aurantium</i>	B	A	A	B	B	B	A	B	C	A	A	B	C	B	B	A	B	A	A	B	E	A	A	A	A	B	A	A	D	A	B	C	A			
<i>Tethya stolonifera</i>	A	A	A	B	B	C	A	B	B	A	C	B	C	C	B	A	B	A	A	B	A	E	A	A	A	A	B	B	A	C	C	A	B	C	A	
<i>Tethya morioni</i>	B	A	B	B	B	C	A	A	B	D	B	B	C	C	A	A	A	B	B	A	A	E	A	A	A	A	B	A	A	C	C	A	A	B	C	A
<i>Tethya bullae</i>	A	A	C	A	A	?	A	A	D	A	B	C	A	A	A	A	B	B	A	A	E	A	A	B	A	B	B	A	D	C	A	A	D			
<i>Tethya australis</i>	B	A	B	B	B	B	B	D	C	B	B	A	C	C	B	A	B	B	B	A	B	C	A	A	A	B	B	A	B	D	B	D	C	C	A	
<i>Tethya papae</i>	B	C	B	C	C	B	B	D	C	D	B	A	A	C	B	A	B	B	B	A	B	E	B	A	B	B	A	A	B	D	C	F	B	B	B	
<i>Tethya pellis</i>	B	B	C	C	B	A	A	D	C	D	B	A	C	A	C	B	B	B	B	A	B	B	B	A	A	A	B	D	A	D	B	?				
<i>Tethya seychellensis</i>	A	A	C	A	B	B	A	C	A	A	A	C	B	D	B	B	B	B	A	D	A	A	A	B	A	A	B	D	B	E	B	C				
<i>Tethya coccinea</i>	B	B	C	A	A	A	C	A	A	A	A	C	A	A	B	B	B	B	A	B	B	A	A	B	A	A	B	A	B	D	C	E	B	?		
<i>Tethya sollasi</i>	A	B	C	A	A	A	A	C	C	B	C	A	C	B	A	B	B	B	B	A	E	A	A	A	A	A	A	A	C	C	E	B	B			
<i>Tethya robusta</i>	B	B	C	B	A	B	A	?	B	D	A	B	B	?	A	B	B	B	B	A	B	A	A	A	B	B	B	A	B	B	A	B	?			
<i>Tethya fastigata</i>	A	C	B	A	C	?	A	A	C	C	B	A	A	D	C	C	B	B	B	B	C	B	B	A	A	A	A	A	A	A	C	C	D			
<i>Tethya amplexa</i>	A	C	B	A	C	B	A	?	B	C	C	A	C	D	C	C	B	B	B	B	C	A	B	A	A	A	A	A	A	A	C	C	D			
<i>Tethya communis</i>	B	B	B	C	C	?	B	D	C	B	A	A	C	B	A	B	B	B	A	A	B	B	A	A	B	B	B	D	C	D	B	?				
<i>Aaptos</i> sp.*	C	D	D	D	D	D	A	C	A	E	D	B	C	D	C	C	B	B	B	B	E	C	B	B	B	B	B	D	A	A	B	A				
<i>Suberites</i> sp.*	C	D	D	D	D	D	A	C	B	E	D	B	C	D	C	C	B	B	B	B	E	C	B	B	B	B	B	B	D	C	A	B	E			

is monophyletic. If two outgroups are used, there may not be a way of rooting the tree such that the ingroup is monophyletic, it might always contain one of the outgroups. Thus, using two outgroups is a more stringent test of ingroup monophyly.

Putative subgroups within the genus *Tethya* are presented in Figure 44. Character state changes in Figure 44 range in consistency value from 0.200 to 1.000 (Table 4) but those from 0.600 to 1.000 predominantly determine the tree topology. Subgroups of species within *Tethya* are differentiated primarily by megasclere morphology (characters 12, 13), the disposition of interstitial megascleres in the choanosome (10), the form of megasclere tracts (7), and what happens to these tracts in the cortex (8), by oxyspheraster morphology (17, 18, 19) and disposition of the oxyspherasters in the cortex (15), and by the presence or absence and size of oxyasters (22). The regularity or deformity of micrasters (30) is also important. Similarly the boundary between the cortex and choanosome (3) and the width of the cortex relative to the sponge radius separate species groups. Colouration (32) and the mode of asexual reproduction (34) are also significant. The postulated character state transformations and position of the changes on the tree will change with the addition of more species on the tree.

Five monophyletic subgroups are hypothesised with a first group including *Tethya anrantium* and *T. stolonifera*, a second containing *T. mortoni* and *T. bullae*, a third group incorporating *T. sollasi*, *T. coccinea* and *T. seychellensis*, a fourth group including *T. fastigata* and *T. amplexa*, and a fifth group including *T. popae*, *T. communis* and *T. anstralis*. *T. robusta* and *T. pellis* do not fall into any group. With the addition of more species to this analysis it is possible that *T. robusta* and *T. pellis* will either become monophyletic groups containing other species or will be resolved closer to the existing subgroups.

Tethya anrantium and *T. stolonifera* in the first group differ from other *Tethya* described here in having mammillate (18) and concave (19) oxyspherasters, a scalloped cortex-choanosomal boundary (3), and radiating but unbranched megasclere tracts (8). The two species also have a peripheral palisade of interstitial spicules in the choanosome (10). Oxyspherasters are present in the upper to middle layer of the cortex (15). *Tethya anrantium* has a relatively wide cortex (6) compared to that of *T. stolonifera* and *T. mortoni* and *T. bullae* in the second group. *Tethya stolonifera* has micrasters with well developed

Table 4 Exploratory phylogenetic analysis of Southwest Pacific *Tethya*. Data from the phylogenetic analysis are listed below. The character number, as given in Table 2, is followed by the number of character states. The column headed Status refers to whether the character was coded *a priori* well defined or questionable. The character states of the basal branch for all *Tethya* species is given along with the plesiomorphic states of the ingroup plus the outgroup. Character weights are listed from Farris (1969) successive approximations weighting procedure.

Character number	Number of states	Basal Branch States for <i>Tethya</i>	Symplesiomorphies (Ingroup + Outgroup)	Consistency value	Weight	Status
1	3	b	?	0.333	996	Q
2	4	a	?	0.500	3374	WD
3	4	d	d	0.750	11390	Q
4	4	b	?	0.500	3374	Q
5	4	b	?	0.500	3374	Q
6	4	c	?	0.600	5831	Q
7	2	a	a	1.000	26999	WD
8	4	c	c	0.750	11390	WD
9	3	b	b	0.286	631	WD
10	5	e	e	0.667	8011	WD
11	4	a	?	0.429	2131	Q
12	2	b	b	1.000	26999	WD
13	3	c	c	0.667	8011	WD
14	4	d	d	0.429	2131	Q
15	4	c	c	0.600	5831	WD
16	3	a	?	0.500	3374	WD
17	2	b	b	1.000	26999	WD
18	2	b	b	1.000	26999	WD
19	2	b	b	1.000	26999	WD
20	2	b	b	0.333	996	Q
21	2	a	?	0.250	421	WD
22	5	e	e	0.667	8011	Q
23	3	a	?	0.400	1727	Q
24	2	a	?	0.250	421	Q
25	2	a	?	0.250	421	Q
26	2	a	?	0.200	215	Q
27	2	b	b	0.333	996	Q
28	2	b	b	0.250	421	WD
29	2	a	?	0.250	421	WD
30	4	d	d	0.600	5831	WD
31	3	c	c	0.286	631	Q
32	6	a	a	1.000	26999	WD
33	3	b	b	0.500	3374	Q
34	5	a	a	0.667	8011	Q

centrums (30), a feature shared with *T. mortoni* in group II and *T. sollasi* in group III.

Tethya mortoni and *T. bullae* in the second group are differentiated from group I in having a linear cortex-choanosomal boundary (3), oxyspherasters present throughout the cortex (15), and in lacking interstitial spicules (10). The two species also have a non-radiating megasclere arrangement (8) and possess a uniquely additional form of choanosomal oxyspheraster (17).

Before the branch point for *Tethya robusta*, a new spicule category appears, the oxyaster (22). The relative width of the cortex also increases from 8 to 9.6% to 13 to 22% of the sponge radius (6) and remains within or above this range in subsequent groups. Collagen is present throughout the cortex (2). In groups I and II collagen is

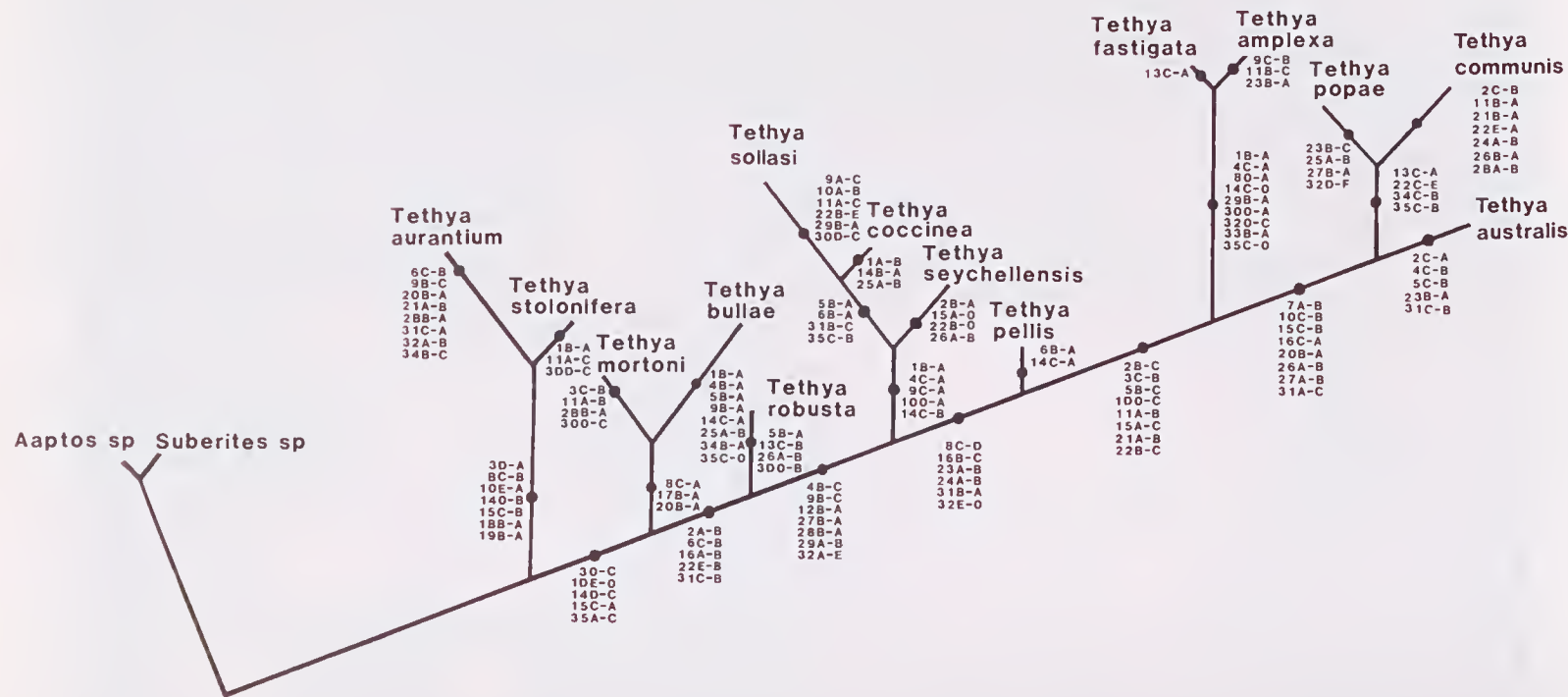


Fig. 44. Hypothesised relationships within the genus *Tethya*. The tree is constructed using weighted branch lengths where the branch length is equivalent to the sum of the consistency values for character changes occurring along the branch. Branch lengths are not proportional to a time period. The hypothesised changes in character states along each branch are given as the character with numbering as in Table 2, followed by the change that occurs from one state to another. Character state changes along the basal branch for the entire genus *Tethya* have been included for convenience in Table 4. Plesiomorphic character states for the ingroup *Tethya* plus the outgroup, are listed in Table 4.

present only as a basal layer in the cortex. Oxspherasters are present in the choanosome as in previous groups but they are smaller in size than the cortical oxspherasters (10). The megascleres of *T. robusta* are flexuous (13) and micrasters can be deformed with the reduction of their rays to stumps.

Further features separate *Tethya robusta* from a third group which contains *T. seychellensis*, *T. coccinea*, and *T. sollasi*. Colour in life changes from orange yellow to pink (32) colouration which is lost in alcohol. Megascleres are stepped at their distal ends (12), species in preceding groups do not have stepped megascleres.

In the third group interstitial megascleres form a peripheral palisade in the choanosome of *T. seychellensis* and *T. coccinea*. *Tethya sollasi* has interstitial megascleres throughout the choanosome (10) and also lacks oxyasters (22) which are present in *T. coccinea* and *T. seychellensis*. *Tethya coccinea* and *T. sollasi* are separated from *T. seychellensis* in the relative width of the cortex which is increased from 13.6% (6) in *T. seychellensis* to 24 to 40% of the sponge radius in *T. coccinea* and *T. sollasi*, a feature shared with only *T. pellis*. *Tethya coccinea* and *T. sollasi* also have a oxspheraster packed cortex (15) whereas in *T. seychellensis* oxspherasters are confined to the upper and lower cortex.

Between group III and *Tethya pellis* several changes occur. Pink colouration is retained, but the colour is stable in alcohol (32) and megasclere tracts exhibit tertiary branching (8). This character state is shared by all subsequent species except *T. fastigata* and *T. amplexa*.

Several character changes separate *Tethya pellis* from *T. fastigata* and *T. amplexa*. The cortex-choanosomal boundary shows a distinctive shallow and irregular scalloping (3). Oxyasters are larger than in previous oxyaster-containing species (22) and the rays can also be branched. Collagen is dense throughout the cortex and choanosome (2). *Tethya amplexa* and *T. fastigata* have deformed microscleres (30) and both species lack oxspherasters (14). These sponges have a non-branched megasclere arrangement as is seen in group II (18) and interstitial spicules are orientated basally in the choanosome above the spicule core (10). This group reproduces by the production of internal buds (34). The megascleres of *T. fastigata* are curved, a feature shared with *T. popae* and *T. communis*.

In a fifth monophyletic group containing *Tethya popae*, *T. communis* and *T. australis* megasclere

tracts are sinuous (7) and exhibit tertiary branching (8) in the cortex. Interstitial spicules (10) are found throughout the choanosome in all three species. Oxspherasters are present but occur in the upper to middle cortex only (15). *Tethya popae* and *T. communis* differ from *T. australis* in having curved megascleres (13), a feature shared with *T. fastigata*. Both *T. communis* and *T. australis* have oxyasters (22) but these spicules are absent in *T. popae*. *Tethya popae* is bright burnt-orange superficially (32) whilst other species in this group are pink.

The low consistency values of several characters (consistency values 0.200 - 0.500) suggests that these characters have a higher rate of change over evolutionary time than the characters with higher consistency values. Whilst the morphology of oxspherasters and the disposition in the cortex appears to be significant in determining the tree topology, oxspheraster diameter (14), presence/absence and size in the choanosome (16) and form, whether long-rayed or short-rayed, (20,21) is not. Similarly the form of the megascleres at their proximal end (11) and what these spicules do at the sponge surface is also unimportant. Microsclere density in the cortex (5) and choanosome (4), the formation of a micraster crust on the sponge surface (23) and micraster category and morphology (24, 25, 26, 27, 28, 29) do not play a significant part in differentiating subgroups of species. Although the depth of the cortex and the disposition of spicules within it are significant, whether the cortex is lacunar or solid (1) and how collagen is distributed within the cortex are relatively uninformative about species group divisions. Sponge size (31) and habitat (34) are equally uninformative. Whilst not so important in revealing relationships between the species of *Tethya* these characters are useful for specific diagnoses.

The phylogenetic hypothesis in Figure 44 does not separate *Tethya communis* from other *Tethya* species as would be expected if *T. communis* was a species of the genus *Tethyorrhaphis*. If we were to retain *Tethyorrhaphis* we would also need to accord the same status to all other monophyletic groups within the genus.

Tethya communis appears as another species of the diverse genus *Tethya*, within which it is included in a group that contains *T. popae* and *T. australis*. These species and *T. communis* have sinuous megasclere tracts with tertiary branches in the cortex and interstitial megascleres throughout the choanosome. The group also includes *T.*

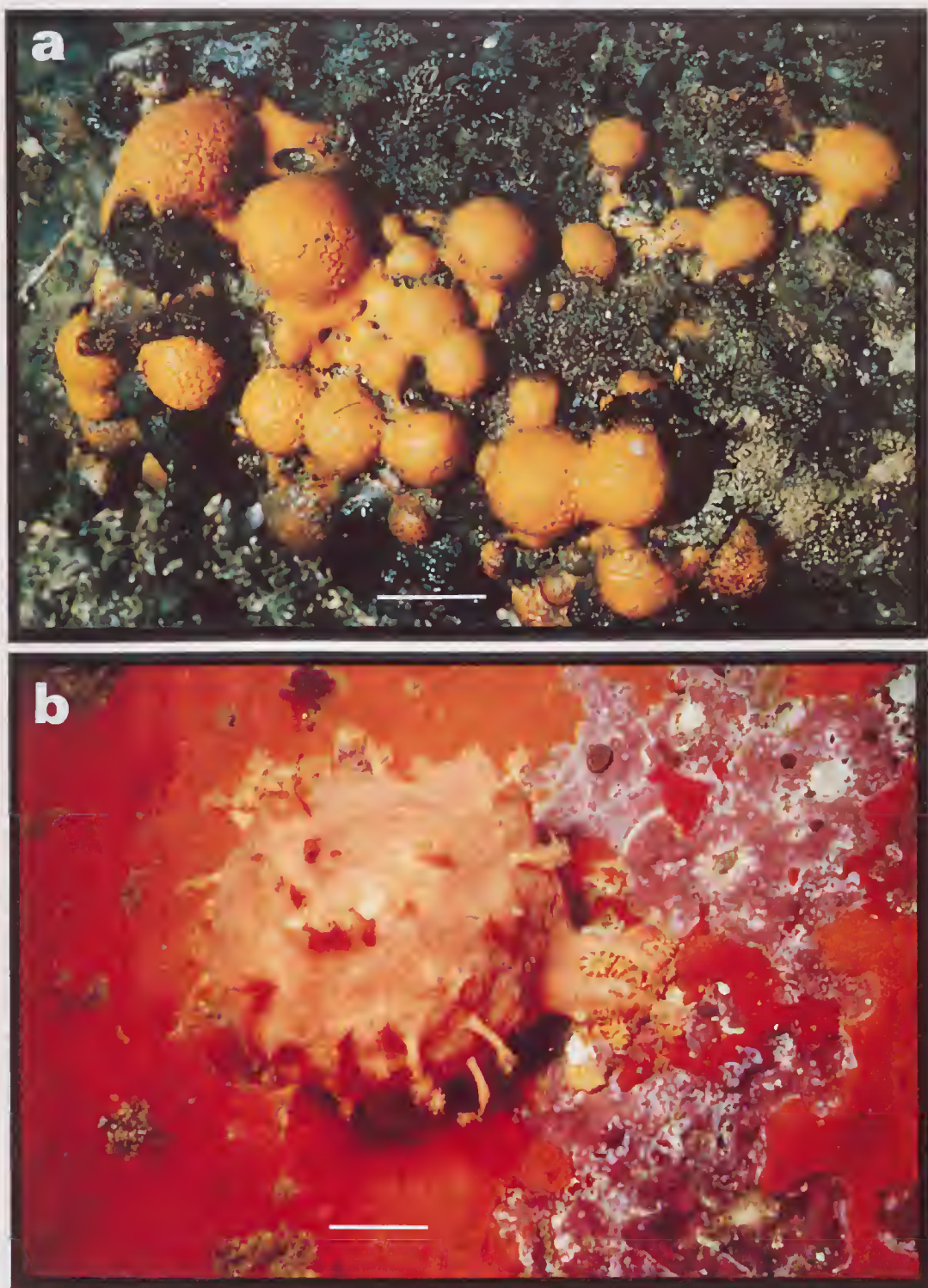


Plate Ia. *Tethya stolonifera*; b. *Tethya australis*, scale = 1 cm.

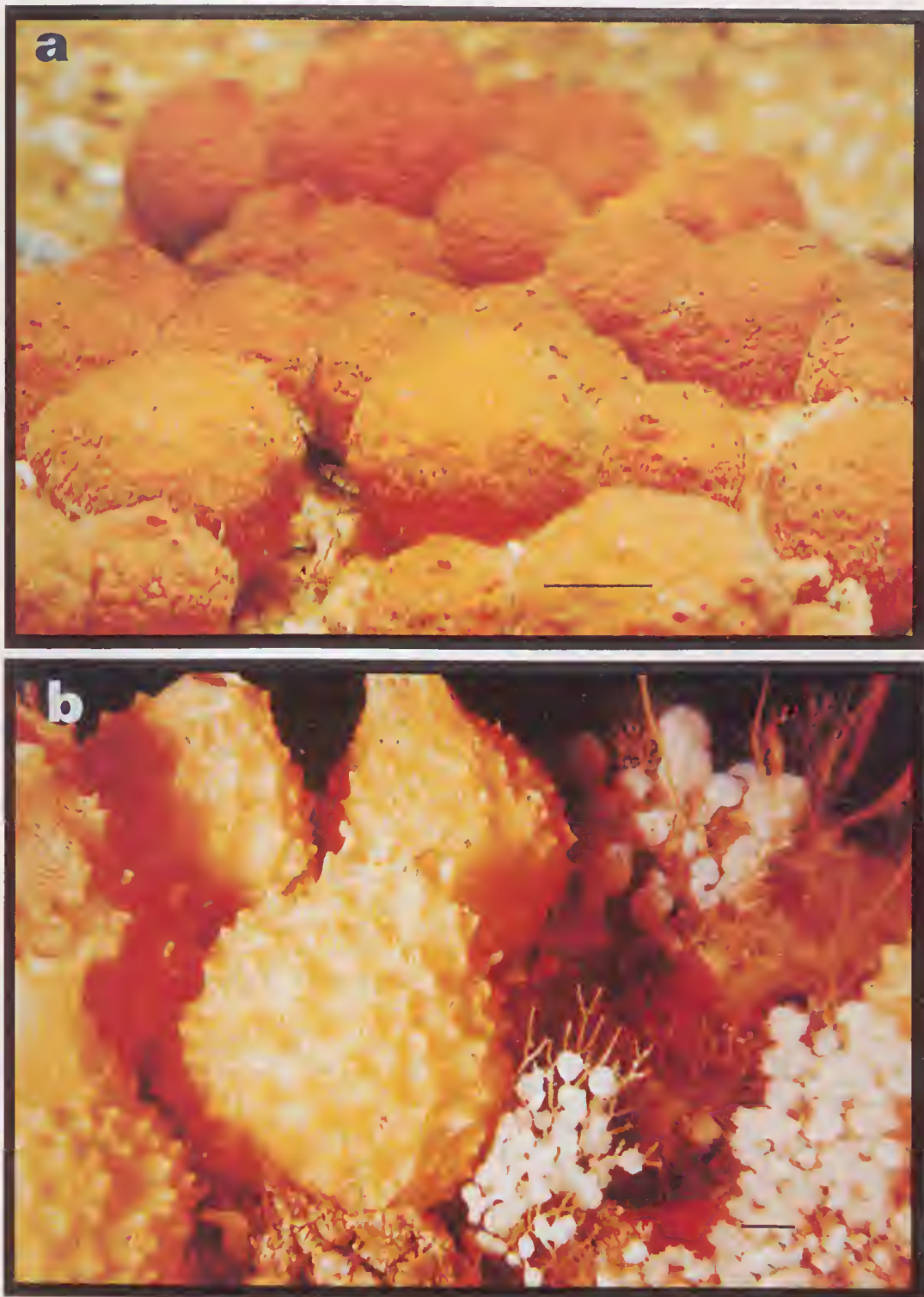


Plate IIa. *Tethya popae*; b. *Tethya fastigata*, scale = 1 cm.

fastigata and *T. amplexa* which contain deformed spicules in a surface crust as is formed in *T. communis*. All species in this group have a low microselere content.

We have not tried to reconstruct the evolutionary history of *Tethya* by inferring loss or gain of particular sets of characters, or to infer character transformation series within *Tethya*, or to ascribe adaptive significance to particular morphologies. In the absence of molecular data, and having only a small number of well described entities we can only confirm that the genus *Tethya* is heterogeneous with recognisable subgroups which are supported by morphological data. Further descriptions of old and new species from a broader geographic range and integration of molecular data with morphological data, in the future, may ultimately enable decisions to be made on the status and range of the species groups present within the entire genus *Tethya*.

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